





MONOGRAPHS ON EXPERIMENTAL BIOLOGY

EDITED BY

JACQUES LOEB, Rockefeller Institute

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LABYRINTH AND EQUILIBRIUM

BY

SAMUEL STEEN MAXWELL, M.S., PH.D.

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BY

SAMUEL STEEN MAXWELL, M.S., PH.D.

PROFESSOR OF PHYSIOLOGY IN THE UNIVERSITY OF CALIFORNIA

ILLUSTRATED



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EDITORS' ANNOUNCEMENT

THE rapid increase of specialization makes it impossible for one author to cover satisfactorily the whole field of modern Biology. This situation, which exists in all the sciences, has induced English authors to issue series of monographs in Biochemistry, Physiology, and Physics. A number of American biologists have decided to provide the same opportunity for the study of Experimental Biology.

Biology, which not long ago was purely descriptive and speculative, has begun to adopt the methods of the exact sciences, recognizing that for permanent progress not only experiments are required but quantitative experiments. It will be the purpose of this series of monographs to emphasize and further as much as possible this development of Biology.

Experimental Biology and General Physiology are one and the same science, in method as well as content, since both aim at explaining life from the physico-chemical constitution of living matter. The series of monographs on Experimental Biology will therefore include the field of traditional General Physiology.

JACQUES LOEB,
T. H. MORGAN,
W. J. V. OSTERHOUT.

PREFACE

It has been the aim in this little volume to present an objective study of the equilibrial reactions of vertebrate animals and the mechanism through which these reactions are produced. Discussions of the possible subjective sensations in connection with labyrinthine excitation, and of clinical applications of the facts are both outside the scope of the book.

The ears of fishes have proved to be in many ways the most favorable objects for these investigations. My own experiments on the functions of the different portions of the labyrinth, especially of the otoliths, were possible only because of the large size and the accessibility of the structures concerned. For these reasons the following pages are devoted largely to the description of the experiments on the ears of selachians and the statement of conclusions which may be reached from these experiments. No safe inferences can be drawn, however, without consideration of the results in all classes of vertebrates. It was the original intention to add a chapter on the effect of repeated rotations, but the interesting work of Griffith indicates that such a discussion would be premature. For a similar reason the developmental studies of Streeter have not been included.

The writer avails himself of this opportunity to express his life-long obligation for both encouragement and inspiration to his teacher and friend, Professor Jacques

Loeb. Thanks are also due to Professor T. C. Burnett, who has kindly read the manuscript, and to Professor E. P. Lewis, whose critical judgment was secured on the physical principles contained in Chapter VIII. Mr. A. M. Hillman gave valuable assistance in the reading of the proof.

S. S. M.

The Spreckles Physiological Laboratory of
the University of California, Berkeley.
January, 1923.

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LABYRINTH AND EQUILIBRIUM

CHAPTER I

INTRODUCTION

Most vertebrate and many invertebrate animals tend to maintain a definite orientation with reference to the lines of gravitational force, or, in everyday language, to keep right side up. If an animal is pushed out of its normal position, changes occur in the tension of the muscles of the limbs or other organs of locomotion in such a way that the original position is automatically regained. When a live fish is rotated around its longitudinal body axis so that the back is turned to the right and the belly to the left, the fins on the right side are at once moved ventrally and those on the left side dorsally. These reflex movements are exactly adapted to restore the body to its normal position of symmetry with reference to the lines of the earth's attraction. To these movements Breuer gave the name compensatory, and to the reaction as a whole Loeb very appropriately has applied the term geotropism.

When the animal is rotated in a horizontal plane, that is, around a vertical axis, compensatory movements also occur, although in this case no new relation has been assumed with reference to the lines of gravitation and the

reaction is not geotropic. For convenience we shall consider these, together with the geotropic reactions, as reactions of equilibrium.

In vertebrate animals the excitations which bring about the reactions of equilibrium arise mainly in the end organs of the eighth nerve, for they may disappear or be profoundly modified when both of the eighth nerves are cut or when both labyrinths are completely destroyed. But very similar compensatory movements occur in animals which do not naturally possess a labyrinth, and they also appear in vertebrates in which both labyrinths have been extirpated.

Compensatory movements can be called forth by moving retinal images, and righting reactions can result from contact stimuli. Also two or more sets of influences may combine to produce the observed effect. Loeb has shown, for example, that in the horned lizard, *Phrynosoma*, compensatory movements of the head may be produced through excitations arising in the retina without the participation of the labyrinth, and also through excitations of the endings in the ears when the eyes are closed. When *Phrynosoma* is rotated with the eyes open, the retinal and labyrinthine stimuli reënforce each other during the rotation, but their after effects are in opposite directions.

The righting reactions of vertebrates are often assumed to be dependent on the labyrinth. A dogfish in which both labyrinths have been destroyed swims with no definite orientation while near the surface, but rights itself promptly if it happens to touch the bottom; hence it will not do to assume that in the normal animal the righting reaction is always due to the internal ear.

The facts just mentioned show that it is necessary to discriminate carefully between those compensatory movements which do and those which do not arise from excitations in the ear. It is important also to determine what part is played by each, where two or more act simultaneously. Contact stimuli, in particular, play so large a rôle that it has seemed desirable to devote a separate chapter to the consideration of reactions of non-labyrinthine origin.

It will be convenient to distinguish, as did Mach and Breuer, between two kinds of equilibrial functions; the one, dynamic, in response to movements of rotation, and the other, static, by which is produced a definite orientation with reference to the lines of gravitational force. We may further recognize the possibility of investigating these functions either through the study of their objective signs in the form of compensatory motions and compensatory positions, or through their subjective manifestations as sensations.

It is self-evident that the subjective method can be used only in man, where operative procedures to determine which functions are lost and which persist after the destruction of certain parts are, of course, out of the question. Moreover the subjective method introduces the difficulty, at times apparently insuperable, of distinguishing between feelings which may properly be termed sensations and the more complicated psychic processes of the nature of judgments. There is, too, the obvious danger that a movement may be interpreted as the effect of a sensation, whereas the sensation may have been the result of the movement, or the two things, sensation and

movement, may have been simultaneous effects of a common cause.

For the reasons just stated, the emphasis has been laid in these studies on the objective method. It has not seemed necessary or desirable to attempt to imagine the sensations of the experimental animals. To say, for example, that the animal feels dizzy, is to make an assumption than can neither be proved nor disproved; while to say that the eyes show a particular form of nystagmus, is to state something which any competent observer may definitely confirm or deny.

CHAPTER II

COMPENSATORY MOTIONS AND COMPENSATORY POSITIONS

THE compensatory movements which are excited by rotational changes of position differ in different animals, in ways dependent largely on the various modes of locomotion and the relative motility of different members of the body. Two characteristics of the movements, however, are remarkably constant; they tend (1) to retain the field of vision existing at the beginning of the rotation, and (2) to restore the body to its original orientation in space.

When a fish is rotated, the reaction is seen in movements of the eyes and fins. If a frog is placed on a turntable, the first response to rotation to be observed, is a turning of the head in a direction contrary to that of the movement of the table. As the rotation continues, changes of position of the limbs occur, and, finally, the animal begins to walk in a direction contrary to the motion.

A pigeon responds to rotation at first by a very decided contrary movement of the head. This continues till a maximum angle has been reached, when a sudden, jerking motion brings the head back toward the median line, and then the compensatory movement begins over again. In this way a more or less uniformly rhythmical succession of compensatory and return movements is kept up. These repeated movements are called *nystagmus*. The

pigeon's eyes also show a nystagmus of the same character as that of the head. The eye movements become more pronounced if the compensatory movements of the head are prevented.

The compensatory movements of reptiles, as described by Loeb¹⁴⁵ in the horned lizard, *Phrynosoma*, and by Trendelenburg and Kühn in snakes and turtles, are in the main very similar to those of birds.

In mammals the compensatory motions are not different in essentials from those of other vertebrates. Mice, guineapigs, and rabbits on a turntable respond to rotation first by compensatory movements of the head and of the eyes, and on continued rotation, if the rate is not too great, by walking in a circle in a direction contrary to the motion of the table. The eye movements usually take the form of a nystagmus, which is more pronounced if the head is not allowed to turn on the neck. In man compensatory motions of the head are not likely to occur but the eye nystagmus is characteristic. In young infants, however, Bartels²⁴ found that compensatory movements of the head occur regularly. Sleeping infants and infants prematurely born show compensatory movements of the eyes but no nystagmus.

In the foregoing paragraphs reference has been made to the reaction which occurs during rotation. When the rotary movement is arrested an after-reaction usually takes place in a direction opposite to that which occurs during the rotation. The after-reaction may consist merely in a return to the normal, resting position, or it may be even as pronounced as the original reaction, but in the opposite sense. Thus when a rabbit is rotated to the right, the head goes to the left, and at the same time

a nystagmus of the eyes occurs with the slow movement to the left. When the rotation is checked the head goes to the right, usually only far enough to return to the midline, and at the same time an eye nystagmus of some seconds duration sets in, with the slow component to the right.

The statements just made refer to movements in the horizontal plane. All the reactions are, in the terminology of Mach, dynamic in character, that is, they are responses to movement; they disappear after the effect of the movement has subsided. Rotations in planes other than the horizontal also give rise to movements which are compensatory in the plane of the rotation, and, in so far, are dynamic; but if the rotary movement is stopped and the body is held in the abnormal position which has been reached, the compensatory position is retained. Thus if a dogfish or a rabbit is held with the body in the normal horizontal position, and is then rotated to the right around the horizontal axis of the body, so that the right side is inclined downward and the left side upward, a compensatory movement of the eyes occurs; the right eye is elevated and the left eye is depressed; but if the body continues to be held in the inclined position thus attained, the unsymmetrical position of the eyes is retained. In this, then, is seen both a dynamic reaction to the effect of the movement, and a static effect as the result of the sustained abnormal position.

The static reactions, or compensatory positions, occur in all classes of vertebrates. In birds and fishes they have long been recognized. Their exact study and description in mammals has been more recently contributed by Magnus and his co-workers.

For experiments on the equilibrial functions of the labyrinth, elasmobranch fishes present many advantages. On account of the cartilaginous structure of the skull, operations may be performed with relative ease, and without disturbance through bleeding. The different parts of the labyrinth are large and are so situated that each may be stimulated or extirpated without necessary injury to the others. The animals are easy to keep quiet during operation and survive the effects well. For these reasons a more complete account of the reactions of the dogfish will be given. The compensatory motions of the eyes and fins in the dogfish, as first described by Loeb,¹⁴³ are remarkably constant. Detailed studies of these movements have since been made by Lee,¹³⁷ Kubo,¹³⁰ and others.

So far as I am aware, the dogfish shows no well defined reactions to movement of translation, that is, to movement in a straight line. On the other hand change of direction in the horizontal plane, or change of position with reference to the horizontal plane, calls forth prompt and characteristic responses. Such changes may be regarded as movements of rotation. When the fish which has been swimming in a straight line alters its course to some other in the horizontal plane, that is, to the right or left, the change involves a rotation around the dorsoventral axis of the body. If the animal sways to one side so that, for example, the belly turns to the right and the back to the left, the movement is a rotation around the longitudinal body axis. When the animal changes position so that the head goes downward and the tail upward, or the reverse, a rotation has occurred around the transverse axis.

All changes of position, except movements of translation, may then be regarded as rotations. All rotations

whatever can be referred to movements about one or more of a system of three body axes perpendicular to each other, the longitudinal, the transverse, or right to left, and the vertical, or dorsoventral. When the dogfish is rotated around any one of these axes the eyes move as if to retain their original position in space, or to preserve the original visual field, while the fins move so as to tend to swing the body back into its original orientation in space. We shall state the reactions to rotations around each of the primary axes separately.

Rotation to the right around the longitudinal body axis, that is, right side inclined downward and left side upward, causes the right eye to move dorsalward and the left eye ventralward (Fig. 1, B.), so that more of the white appears below on the right eye and above on the left eye. Thus in spite of the rotation of the body the two eyes tend to remain in the same horizontal plane. At the same time the right pectoral fin moves ventrally, its posterior margin more than its anterior, and the left pectoral moves dorsally, its posterior margin more than its anterior. The pelvic fins make a similar though less vigorous change of position. In this way the fins are given a screw-like set, so that if the body were propelled forward through the water the effect would be to cause a rotation to the left around the longitudinal axis. Thus the rotation calls out reflex movements of the fins exactly suited to effect a counter-rotation. Rotation to the left around the longitudinal axis causes eye (Fig. 1, A.) and fin movements which are exactly the reverse of those just described.

When the fish is rotated around the transverse axis in such a way that the head goes upward and the tail downward the eyes make a rotational movement on their axes

in a direction contrary to that of the body (Fig. 1, C.), or, in other words, the anterior pole of each eye-ball goes downward and the posterior pole goes upward. The movement is such as would be made if the eyes were wheels on which the body was rolled forward, and hence

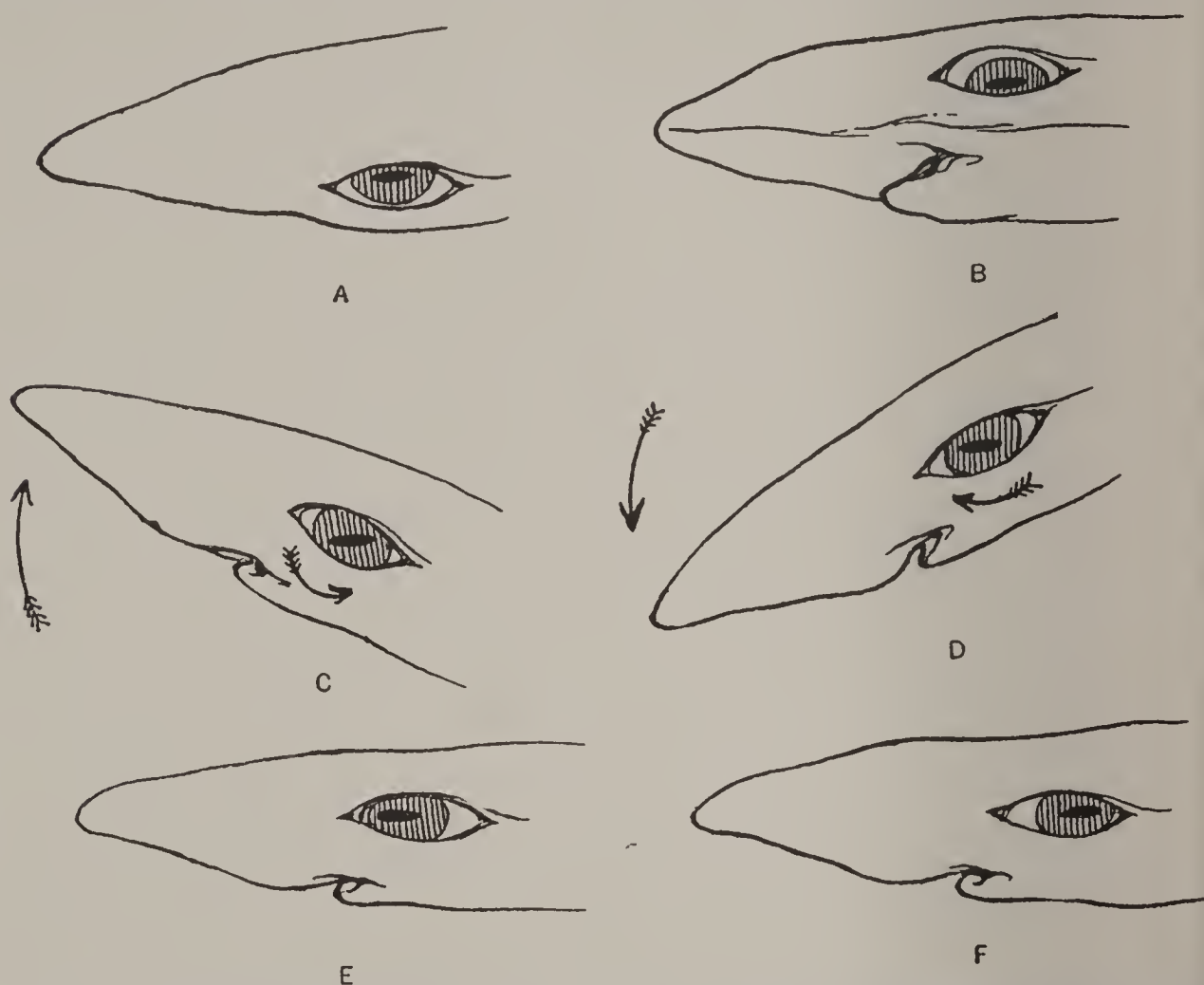


FIG. 1.—Diagrams of compensatory positions of eyes of dogfish; A, rotation to left and B, rotation to right around longitudinal body axis; C, rotation head upward and D, rotation head downward around transverse body axis; E, rotation to left and F, rotation to right around dorsoventral axis.

for brevity I shall describe it hereafter by saying that the eyes roll forward on their axes. At the same time the pectoral fins move ventralward, their posterior margins more than their anterior. The pelvic fins also move slightly ventralward. If the body was moving forward in the water this set of the fins would bring it back from the inclined position to the horizontal. Rotation of the

body around the transverse axis toward the head down position causes the eyes to roll backward on their axes (Fig. 1, D.), and the paired fins to move dorsalward.

The responses to rotations around the longitudinal and the transverse axes are both dynamic and static; that is to say, the compensatory positions are retained if the animal is held in the abnormal position arrived at as the result of the rotation.

When the dogfish is rotated around a vertical axis, that is, in the horizontal plane, the two eyes make a conjugate movement in the direction opposite to the rotation. If the head is turned to the right, both eyes go to the left (Fig. 1, F.); if the head is turned to the left, both eyes go to the right (Fig. 1, E.). Compensatory motions of the fins occur at the same time; when the fish is rotated to the right the dorsal fins move to the left and the caudal fin may also move to the same side. This arrangement of the fins is an effective steering apparatus to guide the course to the left, hence to counteract the effect of the rotation to the right. These reactions are dynamic only; the positions are not retained after the cessation of the rotation which provoked them, even if the animal is held in the new position which has been attained by the rotation.

The effects of rotations in planes other than the primary are readily resolved and are seen to be the resultant of simultaneous rotations around more than one of the primary axes. Thus the body may be rotated in a vertical plane around an axis which intersects the longitudinal axis so as to extend to the left anteriorly and to the right posteriorly. If the animal is rotated around this axis so that the head goes obliquely down and to the right, the

right eye goes up and the left eye goes down (the reaction to rotation around the longitudinal axis), while both eyes roll backward on their axes (reaction to rotation head downward around the transverse axis). Rotation head downward and to the left causes the left eye to go up, the right eye to go down, and both eyes to roll backward on their axes.

Rotation head upward and to the right causes the right eye to go up, the left eye to go down, and both eyes to roll forward on their axes. Likewise, rotation head upward and to the left causes the left eye to go up, the right eye to go down, and both eyes to roll forward on their axes.

The compensatory motions of the fins to rotations around oblique axes may also be resolved in the same way.

CHAPTER III

FORCED POSITIONS AND FORCED MOVEMENTS

THE facts described in the preceding chapter show that a mechanism exists through the action of which animals tend to maintain a definite position with reference to the lines of gravitational force. Any departure from that position calls forth changes in the tension of the muscles in such a way that the eyes and the locomotor organs are no longer held in a symmetrical position with reference to the body of the animal. When a dogfish is held with its longitudinal axis horizontal, but with its right side inclined downward, the muscles which, by their contraction, lower the right eye, act less strongly than when the fish is in the normal position. The reverse state of things occurs in the muscles of the left eye; the muscles which elevate it act less strongly than when the fish is in the normal position. The result of these alterations of muscle balance is, that the eyes are compelled to take an unsymmetrical position with reference to the body. At the same time the paired fins also are placed in an unsymmetrical position through the unequal tension of the muscles on the two sides.

These changes of muscle tension take place just as well in an animal in which the higher parts of the brain, the cerebral hemispheres, have been removed. They cannot therefore be attributed to volition, or to a conscious effort to avoid or to change a disagreeable sensation. They are determined with precision both as to amount

and kind by the amount and kind of movement or change of position by which they have been called forth.

Similar unsymmetrical distributions of muscle tonus can be caused by brain injuries of various kinds. They occur as the result of one sided injury to the medulla, the pons, the optic lobes, the corpora striata, and the cerebral hemispheres. When these effects are due to brain injury, however, the inequality of muscular power is permanent, and the resulting positions and movements are known as forced positions and forced movements.

The experiments of Magendie, Flourens, Vulpian, Luciani, and others have made familiar the effects of one-sided injury to the cerebellum. Luciani's¹⁴⁷ description of a dog in which a part of the right side of the cerebellum has been extirpated shows that an unsymmetrical distribution of muscle tonus and strength is a marked symptom, especially in the first few days after the operation. The fore limbs are stretched out, the right more than the left, the vertebral column curves to the right, and when the animal is again able to walk it can not go in a straight line, but when it attempts to do so, curves off to the right, that is, makes circus movements. When the injury is more extensive, involving the middle peduncle, violent forced movements occur, the animal rolling around the long axis of the body. Forced positions and forced movements of the eye-balls, in the form of nystagmus also result.

We are not concerned here with the old controversy as to whether these consequences of cerebellar injuries are to be regarded as the result of irritative processes or as true deficiency phenomena. Whatever the cause, it is evident that in its attempts at voluntary movement the

animal makes motions and assumes positions that were not intended, and that these differ in a definite way from the movements willed. It is evident, too, that one result of the destruction of a part of the cerebellum is a permanent weakness of certain muscle groups.

Where circus motions occur, they must result from inequality of muscle force on the two sides of the body. When an animal curves to the right in walking, the deviation could be due to an increase of power in the muscles of the legs on the left side or to a decrease on the right side. There is a third possibility, namely, that an increase of power on the one side may be accompanied by a decrease of power on the other. When, however, the unsymmetrical action is caused by the loss of a portion of the brain, but one possibility exists: As has been pointed out by Loeb,¹⁴⁶ "a permanent *decrease* but not a permanent *increase* in the tension of the muscles can result from the destruction of one part of the brain."

The effects of cerebellar injury appear mainly on the side of the operation, because apparently, the fibres concerned do not cross to the opposite side. But a decussation, or crossing over, of the fibres does take place from many parts of the brain so that destruction on the right side has its effect on the left side of the body and *vice versa*. Even the same part of the brain may have different connections in different animals. Thus Loeb^{141, 126} found that in the rabbit injury to one cerebral hemisphere causes circus motions toward the sound side, while a similar operation in the dog causes circus movements to the injured side.

Instead of a complete decussation there may be only a partial crossing of the fibres, so that the effects of the

lesion appear on both sides of the body. This condition is well shown by experiments on the dogfish. Loeb found that when the right side of the medulla is injured at the level of the entrance of the eighth nerve, there occur rolling movements to the right around the long axis of the body. When the animal comes to rest, the body is inclined to one side so that the right side is lower than the left. The eyes and fins are in forced positions, which can be described as a rotation around the long axis of the body. The right eye is depressed, that is, turned more ventrally, while the left eye is elevated or turned more dorsally. The forced position of the fins is just the reverse; the right pectoral fin is elevated and the left is depressed.

It is evident that the unsymmetrical position of the eyes which follows section of the right side of the medulla can only occur if the muscles on both sides of the body are affected. The muscles which raise the right eye and the muscles which lower the left eye must act less strongly than their antagonists. The muscles of the fins of both sides also are affected by the unilateral injury. When the left side of the midbrain is destroyed analogous effects are produced. The body is inclined to the right and the animal, in swimming, makes circus motions to the right.

The significance of the phenomena of forced movements for an understanding of the equilibrium reactions is shown by the two following results obtained by Loeb,¹⁴⁴ on the dogfish: (1) Section of the right eighth nerve causes forced positions and forced movements similar to those which are produced by injury to the left side of the midbrain and to the right side of the medulla, and (2)

the circus motions, the rolling, and the associated forced positions of the eyes and fins which are produced by injury to the left side of the midbrain and the right side of the medulla are completely abolished by section of the left eighth nerve.

The brain injuries which have been referred to thus far are unsymmetrically placed as regards the plane of symmetry which divides the body into a right and a left half, and the forced movements which result can be thought of as rotations around one of two axes lying in that plane; they are either rolling movements around the longitudinal axis of the body or circus movements around the dorsoventral axis. Injuries which are symmetrical, that is, which involve equal structures on the right and left, may also give rise to forced positions and motions. These are of such nature that they can be regarded as rotations around the transverse axis of the body.

Extirpation of the occipital lobes of the brain of the dog causes an elevation of the head and an abnormal extension of the forelegs. The animal is unable to go down stairs but can go up stairs. Corresponding operations on the frontal lobes bring about a condition which is just the reverse. The head is held low and the animal shows a strong tendency to keep moving forward. Flourens⁸¹ described the effects of section of the peduncles of the cerebellum in the rabbit. When the posterior peduncles were cut, violent forced movements occurred; the animal sprang backwards or made somersaults backwards. Section of the anterior peduncles caused the animal to hurl itself forwards. It is evident that these movements are analogous to those which are produced by one-sided injuries, only they are in another plane.

Flourens pointed out that cutting the posterior vertical pair of the semicircular canals had the same effect as section of the posterior peduncles of the cerebellum, while cutting the anterior vertical canals gave results similar to those obtained when he injured the anterior peduncles.

Flourens' methods were not suited to give exact knowledge of the functions of the canals, and the inferences he drew as to the connections of the different parts of the labyrinth with the cerebellum have not been justified by later work. Nevertheless his observations show in a striking way the similarity of the forced movements produced through the labyrinth and those which result from injury to the brain. The significance of this similarity is seen with very great clearness in connection with Loeb's experiments described above on the brain and the eighth nerve of the dogfish. When one side of the medulla is injured, or when one eighth nerve is severed, the paired fins assume an unsymmetrical position which gives them the effect of the blades of a screw. If the animal now is propelled rapidly forward in the water, the screw effect of the fins causes the body to roll around its longitudinal axis. Tilting a normal dogfish to one side also causes an unsymmetrical position of the paired fins, which has the same screw effect as that produced by the operations mentioned. Propelling the body forward in the water must therefore produce the same forced rolling. But when the normal animal has rotated far enough to bring it back to its usual position of equilibrium the cause of the forced movement ceases to act and the fins return to their usual positions of symmetry with reference to the body.

The forced positions in the normal animal and in the operated animal are seen to be the same and their effects on the movements of the animals are the same. The essential difference lies in the fact already mentioned, that, in the normal animal, the position is automatically excited by a rotation and is automatically terminated by the counter-rotation which the first induces, while the forced position in the operated animal is more or less permanent.

Forced positions of the fins can also be caused by retinal stimuli and by contact stimuli. The reactions to contact stimuli are very striking and I shall reserve the discussion of them for a later chapter.

CHAPTER IV

THE LABYRINTH AS A WHOLE

1. THE EFFECTS OF DESTRUCTION OF ONE LABYRINTH

THE effects of destruction of one or of both labyrinths, or of section of one or of both eighth nerves, have been described by many investigators and in a great variety of animals. In general, it may be said that the equilibrium disturbances arising from the loss of one labyrinth are very striking and very persistent. The symptoms usually become less obvious after weeks or months, but never wholly disappear.

The detailed studies of Ewald⁷⁵ on the pigeon with one labyrinth removed are so well known that only a brief reference is needed here. Immediately after the operation, certain disturbances of position and movement begin to appear. Among these disturbances are seen a tendency to hold the head obliquely inclined to the operated side. When the bird attempts to walk it may turn or fall, or in extreme cases, roll, to the operated side. The abnormalities of position, especially of the head, gradually become more marked. In the second and third weeks after the operation they are very intense. The head is not merely held in an oblique position but becomes twisted so that the beak points directly upward and the occipital region of the head is below. This extreme posture is not maintained continuously but occurs when the bird attempts to make voluntary movements, and especially when it is excited or frightened. After some months these disturbances almost wholly disappear.

The pigeon runs about in the aviary, eats and drinks in a manner not to be distinguished from the normal animals. Even in flying, the operated and the uninjured birds can hardly be distinguished.

Notwithstanding the apparently complete recovery, Ewald was able to show that after loss of one labyrinth certain permanent effects remain. When, for example, the bird is suspended by the feet, the wing on the operated side is not drawn up so neatly as that on the sound side. The loss of muscular tonus which this indicates, appears more obviously on the operated side, but Ewald's experiments make it clear that muscle groups on both sides of the body are affected. Thus the flexor muscles of the wing on the operated side are weakened, hence the partial extension under the influence of the weight of the wing when the bird hangs head down; but it can be shown that the extensor muscles of the wing on the sound side are also weakened. On the basis of these and other similar differences, Ewald founded his well-known theory of the tonus functions of the labyrinth. The facts of the influence of the labyrinth on muscular tonus are thoroughly established; it is not necessary here to discuss the specific theory of Ewald in detail.

The destruction of one labyrinth or the section of one eighth nerve gives certain results which seem to be common to all classes of vertebrates. Prominent among these are characteristic forced positions of the eyes and head and of the organs of locomotion. The eyes tend to deviate to the operated side; at the same time the eye on the operated side goes slightly downward and the eye on the sound side goes slightly upward. Eye nystagmus is often present for some days, with the slow movement

to the operated side. The head is inclined so that the operated side is lower than the sound side. In animals like the fishes where the head is not movable on the neck, the body is also inclined to the operated side. In amphibians, reptiles, and mammals there is a tendency to extension or adduction of the limbs on the sound side. This is not so readily seen in birds but Ewald has called attention to analogous phenomena in the pigeon. The characteristic forced positions of the fins of operated fishes we shall describe below. As examples of these forced positions and forced movements after loss of one labyrinth, we may refer to the description by Ewald for the frog, to Trendelenburg and Kühn²³³ for reptiles, to Dreyfuss⁷² for the guineapig, to Prince^{200, 201} for the cat, to Bechterew³⁰ and to Wilson and Pike²³⁸ for the dog, to Beyer and Lewandowsky³⁶ for the ape, and finally for very thorough-going studies of the rabbit, guineapig, cat, and dog to Magnus and deKleijn.¹⁶¹

All investigators since Flourens have noted the remarkably violent rolling movements which take place in the rabbit when one labyrinth is destroyed. Magnus and deKleijn¹⁶¹ have been able, by the use of motion pictures, to analyze the rolling. They have shown that the rolling is really a running which is so interfered with by the extreme tonus differences on the two sides of the body that almost no forward progression can be made. Each revolution of the animal is the result of two leaps.

Animals with only one labyrinth, exhibit the righting reaction, but in doing so they seem to turn in one direction only. Thus Fisher and Müller⁸⁰ found that if a cat with one labyrinth destroyed is held up by the feet and dropped, it rights itself during the fall and comes down

on its feet, but that in doing this it always turns toward the operated side. If the left labyrinth has been destroyed the animal turns to the left while falling, and it does this even if it is dropped from the position in which the right side is below. In falling from the latter position the righting could occur either by turning 90 degrees to the right or 270 degrees to the left, but in the absence of the left labyrinth the cat invariably turns through the longer distance, the 270 degrees, to the left and not through the more direct way to the right. An exactly comparable reaction is seen in the dogfish.

The reactions to rotations around a vertical axis, that is, in the horizontal plane, are affected in all these animals but not in exactly the same way, or at least not to the same extent. These differences will be discussed in another connection.

We shall now examine, somewhat more in detail, the effects of this operation on the Selachian.

In the dogfish, section of one eighth nerve or total destruction of one labyrinth give essentially the same results. The behavior of animals so operated was described by Loeb¹⁴⁴ and later by Lee^{137, 138} and others. Their descriptions agree in the main with what one sees in a common dogfish of the Pacific coast, *Mustelus californicus*.

When the right labyrinth of the dogfish is destroyed, the eyes and fins assume forced positions which are more or less permanent. The right eye goes down, that is, it takes a position more ventral than normal, so that the white of the eye is exposed above the iris, while the left eye goes up, or dorsally, exposing more white below the iris. The right eye is also turned slightly posterior, or

tailward, and the left eye slightly anterior. The paired fins are forced into positions opposite to that of the eyes; the pectoral and pelvic fins are elevated on the right side and those on the left side are depressed. The dorsal fins are bent to the left.

In consequence of the forced positions of the fins, attempts at locomotion may cause the animal to roll to the right, around its longitudinal body axis. Circus movements also occur, the animal usually turning to the right, but circus motions to the left may sometimes be seen. After some hours, the animal swims about very much like the other fish in the aquarium, turning sometimes to the right and sometimes to the left. It is seen, however, that the body is inclined so that the median plane is tilted to the right, that is, the right side is inclined somewhat downward and the left side upward. The deviation from the vertical may amount to about thirty degrees.

If the animal is taken from the water and returned belly upward it rights itself at once, but invariably turns to the right in doing so. If one holds the fish in the water and attempts to turn it so that its left side will be down a strong resistance is made, but very little resistance is presented to turning it with the right side down.

When a dogfish with the right labyrinth destroyed, is rotated to the left in the horizontal plane, the eyes and fins give the normal reaction described in Chapter II; the dorsal fins bend to the right and the two eyes make a conjugate movement to the right. When the animal is rotated to the right there is no reaction of the eyes or fins. In general, when the fish is rotated around the dorso-ventral axis to the sound side, the normal reaction occurs;

when the rotation is to the operated side, the reaction is absent. Rotation around the longitudinal axis causes eye and fin movements corresponding to those which occur in the normal animal, but with this difference, that these compensatory movements are superposed on the already existing forced positions; the right eye is already depressed and the left eye elevated, hence rotation to the right around the longitudinal axis merely causes the eyes to be returned part way towards their normal position, while rotation to the left increases the existing asymmetry. Rotation around the transverse axis produces reactions which differ but little from those of the normal animal.

As has been pointed out by Loeb, ^{144, 146} certain muscle groups in the dogfish act as a unit in the equilibrium reactions (and probably in many other movements). Thus we have seen that, in response to rotations around the longitudinal axis, when one eye or one of the paired fins goes up the corresponding member on the other side of the body goes down. When the animal is rotated around the dorsoventral axis the eye movements are conjugated; both eyes look to the left, or both to the right. The asymmetrical positions assumed by the eyes and fins as the result of injury, either to one eighth nerve or to one side of the medulla, can only be the result of tonus changes in muscles on both sides of the body. It might be assumed that the nervous mechanism which controls the paired fins acts as a unit for the two sides and that the muscles of the two eyes likewise act as a unit, so that the one pectoral fin or the one eye can not move without a definitely related movement of its fellow; a tonus change which affects the position of one eye or one paired fin

must therefore produce a related change in position of the fin or eye on the other side. Such an assumption has been rather commonly made for the eye musculature, although it is well known that a certain amount of independent movement of the two eyes is possible even in man. If a prism of small angle is placed before one eye, objects appear doubled because the images no longer fall on corresponding points of the two retinas. But by voluntary effort one can bring the eyes into the position in which the images do fall on corresponding points and the objects appear single once more. Bartels²⁶ and others have shown by kymograph tracings that the two eyes do not react exactly alike to rotation on the revolving table, especially after asymmetrical labyrinth operations.

In the shovel nosed ray, *Rhinobatus*, the equilibrium reactions of the two eyes are beautifully coördinated, and the asymmetrical positions which result from labyrinth injuries are practically the same as those which we have described for the dogfish. The anatomical arrangements are, however, quite different. The eyes of the dogfish are on the sides of the head with their visual axes almost horizontal. The eyes of the ray are on the dorsal side of the broad flattened head, and can be elevated or retracted in a manner which closely resembles the movements of the eyes of the frog. In the frog, however, there is a definite muscle, the retractor bulbi, which is used to retract the eye-ball. The rays do not possess a retractor muscle; the eyes are pulled down by the contraction of some or all of the usual six eye-muscles. It will contribute to the understanding of the nature of the symmetrical eye movements in the equilibrium reactions if we have

a knowledge of the extent of independent motion possible to each eye singly.¹⁷⁵

When a *Rhinobatus* is placed on a shark-board and supplied with plenty of aerated sea water through a rubber tube, little or no tying is necessary to keep it in position. Under these conditions a contact stimulus applied to the upper surface of the head or snout excites certain very definite coördinated movements of the fins and eyes, the particular combination of movements depending on the locus and strength of the stimulus.

If the skin of a *Rhinobatus* is gently stroked with the finger or with a blunt instrument at any point along the midline of the head, for example, between 7 and 8 (Fig. 2), both eyes are retracted, the movements of the two being approximately equal. If a similar stimulus is applied near the outer margin of the upper surface of the head, as at 1 (Fig. 2), the eye on that side is retracted strongly, the other eye is moved very little or not at all. If trials are made at other places, *e.g.*, at 2 or 3 (Fig. 2), it is seen that, as the point stimulated approaches the midline, the amount of movement of the two eyes becomes more and more nearly equal, or in other words, the relative amount of retraction of each eye varies inversely with its distance from the point of application of the stimulus.

It was relatively easy to record these movements graphically. An Engelmann pincette was attached to each eye by a fold of the integument just where the rudimentary lid passes over into the cornea. The pincettes were connected by threads to a pair of light heart levers in such a way that retraction of an eye gave an upward direction to the curve. In the tracing here reproduced, Fig. 3, the upper lever was connected with the left eye

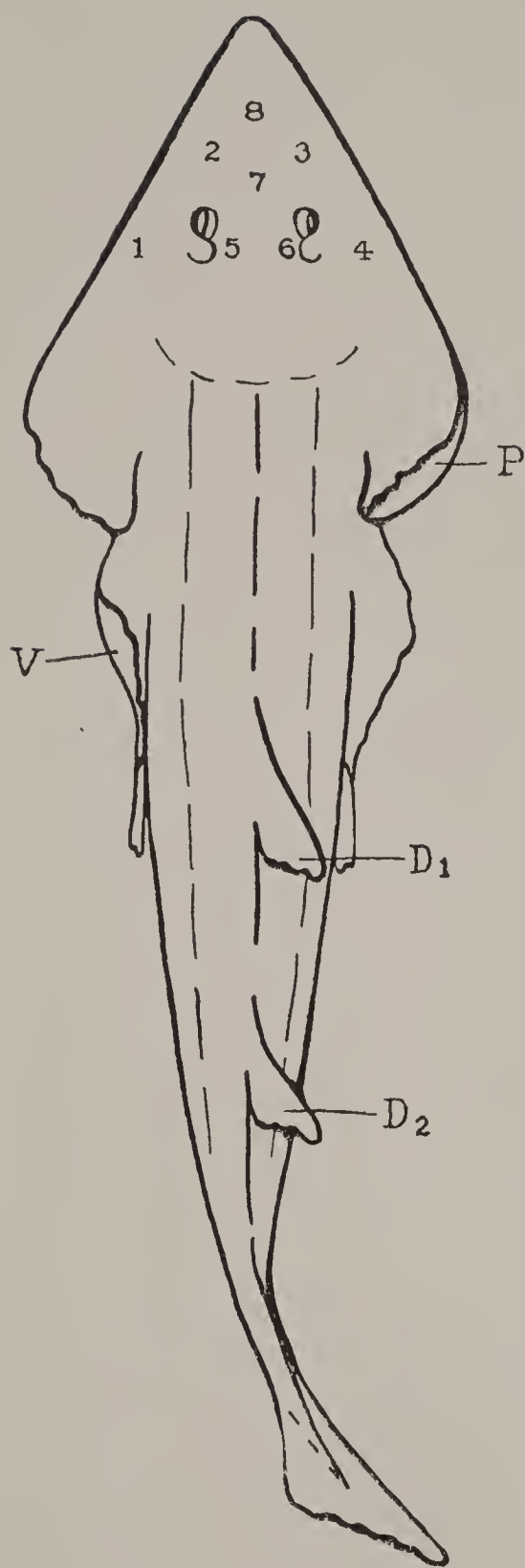


FIG. 2.—Diagram of dorsal view of *Rhinobatus Productus*.

and the lower with the right. The writing points were placed as nearly as possible in the same vertical line, but in order to make the relations more certain, simultaneous ordinates were marked throughout. The small rhythmical oscillations are respiratory, rather than eye movements. Spontaneous, “voluntary” movements occur occasionally, as between 6 and 7, near the end of the tracing. In this experiment the stimulus employed was a gentle stroke with the finger. These strokes were made as nearly equal as possible, but the method could hardly be expected to give perfectly uniform results. The number at the bottom of the tracing show the points stimulated as charted on Fig. 2.

Certain peculiarities should be mentioned. While the responses could be obtained from contact stimuli on all parts of the upper surface of the head, some parts were noticeably more sensitive than others.

Also some parts were less likely than others to produce the bilateral response. Thus the strength of stimulus

used in securing the tracings reproduced, rarely gave rise to a retraction of both eyes when applied at 5 or 6, very near the inner margin of the eye. Stimuli applied to the lower surface of the snout, even near the lateral margin where the upper surface was very sensitive, were very slightly or not at all effective.

The movements which I have just described are retraction of the bulbs and partial closure of the rudimentary lids, and are not at all to be confused with the conjugate movements which result from excitation of the labyrinth.

I have observed the same kind of independent movements of the eyes in all the skates and rays which I have had the opportunity to examine and have made graphic records of these movements in several different genera. It also is probable that the paired fins are capable of much independent movement, but it did not seem important to examine this point because in the higher vertebrates this condition is characteristic.

In the ordinary movements of the eyes as well as of the fins, Sherrington's principle of reciprocal innervation is exhibited. When the left eye is turned to look to the right, the rectus internus of that eye contracts but at the same time the antagonistic muscle, the rectus externus, is not merely passively stretched but definitely relaxes. While this movement is made by the left eye, the right eye moves correspondingly and its movement involves contraction of its rectus externus and relaxation of its rectus internus. In every case in which a pair of body members makes associated movements like those which occur in the fish in response to rotations in the various planes, four muscles or groups of muscles must have

their innervation simultaneously affected. Magnus has shown that in the higher vertebrates also, each labyrinth influences muscle tonus on both sides of the body, and in such a way that the flexors on the one side and the extensors on the other are affected in the same sense; an increase of tonus of the extensors of a right limb is accompanied by an increase in tonus of the flexors of the corresponding left limb. In view of the possibility of free and independent movement of each member separately, this orderly distribution of tonus effects from the labyrinth is especially striking.

2. THE EFFECTS OF DESTRUCTION OF BOTH LABYRINTHS

AFTER section of the two eighth nerves or destruction of the two labyrinths in the dogfish, no definite forced positions or forced movements are seen. The eyes and fins maintain their symmetrical position, and the animal is able to swim in a manner which can appear quite normal. If, however, the fish is placed in the water with the belly up, it swims off in that position and may not right itself for some little time, or it may make irregular rolling movements. When held in the water in the normal position it offers none of the resistance to being passively turned back downward which is so characteristic of the fish possessing both labyrinths. In short, the geotropic reactions appear to be wholly abolished.

Kreidl¹²⁷ gives a similar description of dogfish in which only the otoliths have been destroyed; but he adds that the operated fish when at rest could be quietly turned over with a glass rod and would lie for a long period on their backs. When swimming about the aquarium they came to rest on their backs sometimes and remained in that

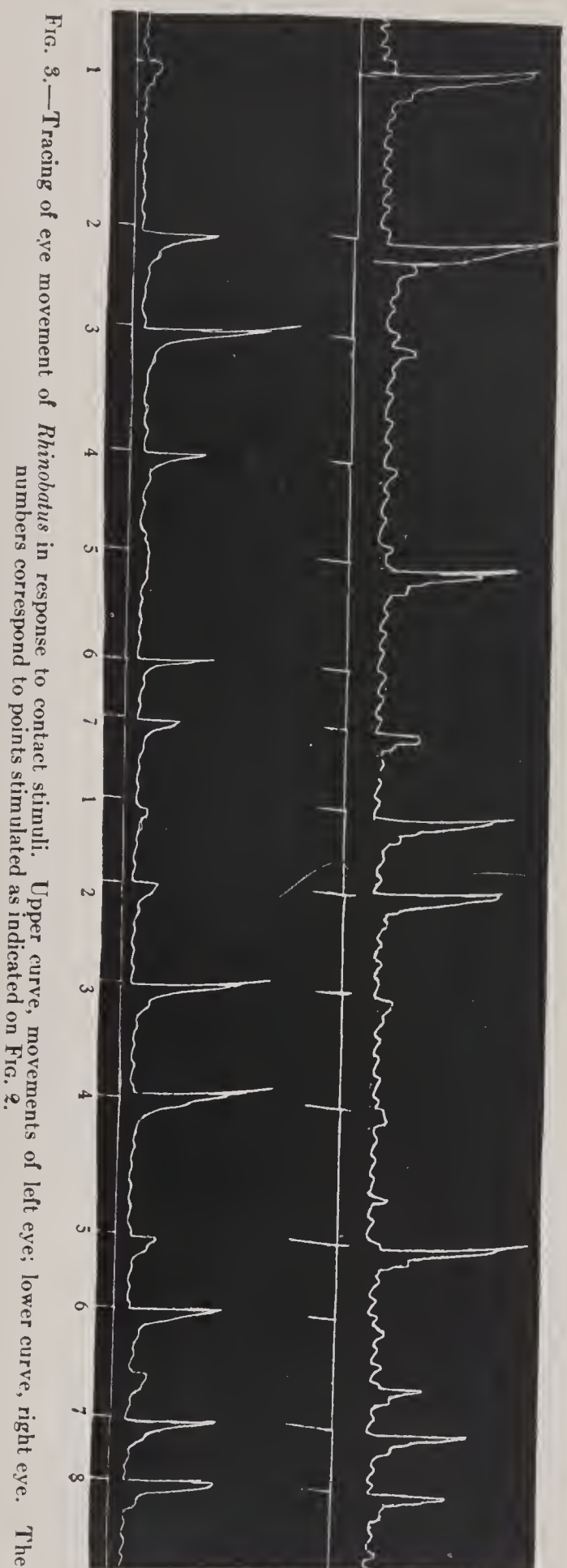


FIG. 3.—Tracing of eye movement of *Rhinobatus* in response to contact stimuli. Upper curve, movements of left eye; lower curve, right eye. The numbers correspond to points stimulated as indicated on FIG. 2.

position. When a number of the operated fish were kept in the one aquarium they often came to rest lying upon one another, any side up, like a heap of dead fish. Lee¹³⁷ gives a somewhat similar account of the effect of section of both eighth nerves. He states, "The animal may be placed upon his belly, his back, or either side without manifesting objection, and, after swimming, he may come to rest in any one of these positions. In reclining he is perhaps most easy in his customary resting position with belly downward, yet he does not appear to be seriously inconvenienced by any other attitude, and, when supported by the side of the tank, has been seen to rest standing on his head."

My observations differ somewhat from those just quoted. Dogfish with both labyrinths completely destroyed will, ordinarily, swim about quietly in a manner hardly to be distinguished from normal animals. Only when greatly or suddenly excited do they show the disturbances of equilibrium described above. Vigorous specimens, in good condition, come to rest in the same position as unoperated fishes. Only when in a moribund state or excessively fatigued do they lie in the abnormal positions described by Kreidl. This matter will be discussed in the next chapter.

Labyrinthless dogfish usually give no reaction of eyes or fins when rotated around any one of the three body axes. In rare instances I have observed a slow compensatory movement of the eyes when the fish was rotated around its longitudinal axis. The movement is much slower than that which occurs when the labyrinth is functional; it occurs so seldom that I have not been able

to investigate it properly, but I believe it to be a retinal reflex. Lyon, however, has described occasional compensatory movements after section of both eighth nerves and both optic nerves as well.

Destruction of the two labyrinths in the frog produces great disturbances of equilibrium. The animal makes violent, disorderly movements when laid on its back, and has great difficulty in righting itself. In the water it is badly disoriented, and rolls around irregularly making little forward progress; the swimming movements are not well executed; the two hind legs make irregular paddling, instead of the usual simultaneous strokes. On land the leaps show disturbances in the use of the voluntary muscles. No equilibrium reactions are seen on the turntable, if retinal images are excluded.

In another amphibian, *Siredon*, Laudenbach¹³² saw, after destruction of both labyrinths, disturbances of orientation and irregular rollings when the animal attempted to swim. When worn out with long continued swimming and rolling, the animal sank to the bottom and lay in any chance position until it was rested; then it oriented itself normally.

In birds, the account by Ewald⁷⁵ of the condition of the pigeon with extirpated labyrinths remains the classic. At first very serious disturbances in the use of the muscles occur. The animals must be given food and drink artificially. At a later stage the birds deport themselves more normally. They run about on the ground, drink, and pick up their food much like the uninjured birds; but they do not fly. When the eyes are covered the head

is held in an abnormal position. On the turntable eye-nystagmus occurs during rotation but no after-effect appears. The eye-nystagmus, however, does not occur when moving retinal images are excluded by surrounding the bird with a gray paper cylinder which rotates with the turntable. Ewald laid great stress upon the fact, proved by many experiments, that in the pigeon, the voluntary muscles are markedly weakened after loss of both labyrinths. This is indicated, among other things, by a seeming looseness of the muscles of the neck which allows the head to swing around freely on account of its own weight and inertia.

Experimental work on the labyrinth of reptiles is not extensive. Trendelenburg and Kühn²³³ have described the effects of destruction of both labyrinths in a lizard, a turtle and a water-snake. The resting position of the operated lizard does not differ from the normal. There is a certain amount of insecurity in rapid movement, so that the animal at times falls or turns over. Lack of skill is seen in climbing and in catching food. The righting reflex occurs promptly, but the muscular movements are not well coördinated and the animal may roll around for a time before getting securely on its feet again. In swimming, the lizard is wholly disoriented and rolls over in all sorts of ways. On the turntable during rotation, the compensatory position of the head is normal and eye-nystagmus occurs, but there is no after-effect either in the form of compensatory position of the head or nystagmus of the eyes. That the reactions during rotation are due to moving retinal images, is shown by the fact that, if the

eyes are closed, neither reaction during rotation nor after-effect on stopping can be detected in the operated animal.

The water-snake, *Tropidonotus natrix*, after loss of both labyrinths seems to creep almost normally, but, on stopping, the head sways from side to side for a time. In the water the snake almost never rolls over, but occasionally may swim in a spiral or figure eight. The loose holding of the head is seen in swimming. The normal snake holds the head and first few vertebral segments straight in the line of progression, while the remainder of the body makes characteristic undulatory movements. The operated snake allows the neck and head also to participate in the side to side oscillations. In the mud turtle, *Emys lutaria*, destruction of both labyrinths produces still less disturbance. Nothing abnormal is seen in the resting position. Laid on its back the animal rights itself like a normal turtle. Orientation occurs both while swimming at the surface and when submerged. There is more swaying while swimming than in the normal animal, but there is no complete disorientation. Compensatory movements are nearly if not wholly absent.

In mammals, as a rule, the disturbances following the destruction of both labyrinths are at first very severe, but they do not present the stormy character of those which follow the one-sided operation. There is no forced position; rolling movements are absent or only very transitory. Dogs and cats are for a time unable to stand. When the head is raised it swings from side to side, making it difficult or impossible for the animal to seize its food. Nystagmus of an irregular sort may persist for a few days. All these symptoms gradually disappear,

until finally there is little in the ordinary behavior, to distinguish the operated from the normal animal. A labyrinthless dog, however, always shows some lack of skill in the use of the voluntary muscles; he is not accurate in catching with his mouth pieces of meat thrown to him, and he tends to slip when he runs on a smooth floor. Moreover, he is disoriented and helpless when his eyes are bandaged. Wilson and Pike²³⁸ found that the dog without labyrinths was likely to roll and tumble about when thrown into the water, but could sometimes orient itself promptly and swim in a fairly normal manner.

CHAPTER V

REACTIONS OF NON-LABYRINTHINE ORIGIN

IF WE turn a planarian worm on its back (dorsal side) it immediately rights itself. The movement has the appearance of a true geotropic reaction; but if the worm is placed with its dorsal side in contact with a vertical surface, *e.g.*, the wall of an aquarium jar, the righting reaction takes place just as well. Even when the planarian, in swimming, comes to the top of the water, a righting reaction occurs in which the organism places itself with its ventral side up, and creeps on the under side of the surface film. It is evident that these reactions are not geotropic; they do not depend on the lines of force of the earth's attraction, but are brought about through the effects of contact stimuli. The worm is so organized that the touch of a solid body against the dorsal surface causes the coördinated muscular movements necessary to turn the animal over and bring its ventral side into contact with the solid.

When a dogfish is turned belly upward in the water it very promptly rights itself. The action takes place under conditions which show that the cause is essentially different from that which produces the righting movements of the planarian, for the fish is surrounded on all sides by a medium which presses equally in all directions and so presents uniform contacts to every part of the body surface. We have seen that under these conditions this reaction fails in a dogfish deprived of its two labyrinths, but that, nevertheless, such a fish rights itself

promptly as soon as it comes in contact with the bottom of the aquarium. There are, then, at least two ways in which the righting reaction of the fish may be brought about, one of them geotropic and the other stereotropic.

When a normal pigeon is rotated on the turntable a nystagmus is produced. If both ears are destroyed, rotation still causes nystagmus, or, if the ears are intact but the animal is blinded, a nystagmus still follows rotation. When, however, the bird is deprived of both eyes and both ears at the same time, rotation no longer excites a reaction. It follows from this that equilibrium reactions may be brought about through retinal stimuli also.

Since reactions which are alike or which have very considerable resemblance may arise from the stimulation of different receptor organs it becomes necessary to study the retinal effects and the contact reactions in the animals which are used for experiments on the functions of the labyrinth.

1. CONTACT REACTIONS

DURING two summers of experiments on dogfish, the animals were kept in a concrete tank ten feet long and six feet wide with a depth of water which varied from one to two feet. The fish sometimes rested quietly on the bottom; at other times they swam round and round, keeping usually near the walls. When dogfish in which both labyrinths had been completely destroyed were placed with the others in the tank their behavior, except when greatly excited, could hardly be seen to differ from that of the normal animals. They swam quietly around or settled on the bottom in normal orientation.

The orientation of the labyrinthless dogfish might have been due to retinal stimuli; that it was not so was proved in the following way: A dogfish in which both labyrinths had been destroyed on the preceding day was observed to orient itself, in swimming, like a normal fish, and to come to rest right side up on the bottom of the aquarium. Over each eye of this animal I sewed a large patch of heavy, black, rubber cloth. This cloth extended on all sides some distance beyond the eye and was stitched directly to the skin of the fish. When the animal was returned to the water its behavior was almost, but not exactly, as before. It swam about with good orientation and never came to rest on the bottom in an abnormal position. Under these circumstances the organism is deprived of two of the three kinds of impulses on which its orientation in space depends. It is now without retinal and labyrinthine stimulation and must rely upon contact stimuli alone.

When the normal dogfish were swimming around the aquarium keeping near to the walls, their bodies were almost always slightly tilted so that the side away from the wall was a little deeper in the water than the side next the wall; the belly was thus turned slightly toward the wall, and usually, too, the first dorsal fin, instead of being held in a position symmetrical to the body, was flexed to the side next the wall. Dogfish which had been blinded and deprived of both labyrinths exhibited this phenomenon, but in a more marked degree. Such animals were frequently seen swimming along the side of the aquarium with their bellies turned directly to the wall exactly as if the wall had been the bottom; *i.e.*, the animals

in swimming were oriented to a vertical instead of a horizontal surface. In this orientation they often swam the length of the tank. It is probable that if the available distance had been greater the weight of the fish would soon have brought it into contact with the bottom.

The foregoing observations made it desirable to investigate in more detail the contact reactions of the dogfish.¹⁷⁶

A dogfish tied down on the shark board and supplied with a current of aerated sea water responded to stroking or scratching stimuli applied to the head or snout with decided movements or changes of position of the fins; but the results were often confusing or contradictory. A contact stimulus applied to the right upper surface of the snout would at one moment cause the dorsal fins to turn to the right, while at another moment a stimulation of the same region caused these fins to bend to the left. The paired fins and the tail participated in these responses, and the direction of their movements had a definite relation to the movements of the dorsal fins. It became apparent that these fin movements were always consistent among themselves; they were more than simple reflexes, and showed a coördinated adjustment of the organism as a whole. In general they could be seen to exhibit such an arrangement as would be necessary to turn the animal either in the direction of the stimulating object or away from it. That is to say, the reactions were in each case stereotropic, but the sense of the stereotropism could be positive or negative. It became then a matter of interest to determine, if possible, the conditions of the reversal, and so to control these conditions as

to make the responses predictable. This proved to be indeed very simple.

In making these experiments on the effects of contact stimuli it would have been desirable to keep the fish in its natural position in the water. This however was impracticable because the mechanical effect of the stroke or push which constitutes the stimulus was sufficient to move the body of the fish under the unstable conditions of water support only. Moreover the stimulus excited movements of locomotion and the observer was unable to keep track of the positions and changes of position of the different fins. If the aquarium used was large the fish was soon out of reach; if small, new stimuli were offered by collision with the walls. Another disturbing factor, if the animal is floating in the water and free to move, is the fact that each response to a tactile stimulus causes such a change of position as to excite the labyrinth and thus introduce other reflexes. It was necessary, therefore, to use the ordinary method of artificial respiration by means of a current of aerated sea water through a rubber tube in the animal's mouth.

When the dogfish is first placed on the shark board rather violent struggles occur, and tying is usually necessary until the animal becomes quiet. After a few minutes of immobility the cords can be gently loosened and removed and the experiment can go on for some time without any need of artificial restraint. This is important because experiments on contact stimuli should not be complicated by possible inhibitions or reënforcements from the presence of the binding cords. It is true that the ventral surface of the body is still in contact with the board, but this is not an unnatural situation since the

animal when free, often rests for long periods on the bottom of the aquarium. In order better to observe the movements of the paired fins, the animal was usually placed above the board on a thick piece of wood no wider than the body, thus allowing the pectorals to project like wings.

The reactions about to be described were obtained by stroking or scratching the outer margin of the head from near the snout to a point just below the eye. It was not necessary that the stroke be carried the whole distance; a short stroke or sometimes a mere touch anywhere within the region mentioned gave the same result. It is not to be inferred that analogous reactions are not elicited by contact stimuli applied to other regions. I have confined this account to reactions from the parts mentioned for the sake of definiteness of description and interpretation.

For most dogfish a stroke with a finger wet with sea water was sufficient to produce a definite response. As a more severe stimulus I used a scratch with the points of a small pair of forceps. The first of these usually corresponds to the designation "weak" the other "strong" stimulus.

It soon became apparent that fairly constant responses could be obtained if the stimuli were of uniform intensity. In fact under favorable conditions the movements could be repeated over and over with machine-like regularity. The following portion of the record of an experiment is typical (Table I.). The pauses between the successive trials were merely the time necessary to set down the results.

TABLE I.

REACTIONS OF A DOGFISH TO CONTACT STIMULI.

Mustelus californicus, 33 Inches Long, May 20, 1921.

Stimulus		Reaction				
Kind	Side	D1	D2	Tail	Right Pectoral	Left Pectoral
Weak (Finger)	Left	Left	Left	Left	Down/	Up\
	Right	Right	Right	0	Up\	Down/
	Left	Left	Left	Left	Down/	Up\
	Right	Right	Right	Right	?	Down/
	Left	Left	Left	Left	Down/	Up?
	Right	Right	Right	?	Up\	Down/
Strong (Forceps)	Left	Right	Right	Right	Down\	Up/
	Right	Left	Left	Left	Up/	Down\
	Left	Right	Right	?	Down\	Up/
	Right	Left	Left	Left	Up/	Down\
Weak (Finger)	Left	Left	Left	Left	Down/	Up\
	Right	Right	Right	Left?	Up\	Down/
	Left	Left	Left	0	Down/	Up\
	Right	Right	Right	Right	Up\	Down/
Strong (Forceps)	Left	Right	Right	Right	Down\	Up/

The first column indicates the strength of stimulus; the second, the side of the head to which it is applied; the third, fourth, and fifth, the direction of movement of the first and second dorsal and the tail fins, respectively. The last two columns give the direction of movement of the anterior border of the right and left pectoral fins; and, in these two columns, / at the end of the word indicates that the posterior end of the fin was higher than the anterior; \, that the posterior margin was lower than the anterior.

Inspection of the results of the above experiment shows that when a weak stimulus is used the dorsal fins and the tail turn toward the stimulated side. The effect of these as a steering apparatus would be to change the

course toward the stimulated side; *e.g.*, turning the dorsal fins or the tail to the left would cause the course to swerve to the left. But in addition to this another effect would result. When a dorsal fin turns to the left it assumes an oblique position; that is, it is its posterior border which goes to the left most strongly. Its resistance as the animal moves forward in the water would have a screw effect, tending to rotate the body around its longitudinal axis so that the ventral side would be turned in the direction of the stimulating object. This rotation effect would be increased by the new position of the pectoral fins. The pectoral on the stimulated side is elevated but its posterior margin is raised less than its anterior or is even depressed; the pectoral of the other side makes a movement which is just the converse. These fins would then also have a screw effect tending to the same direction of rotation as the dorsals, namely, ventral side toward the stimulating object. The reaction is clearly tropic and in the positive sense.

It will be seen that the total effect of a weak stimulus is to turn the ventral side of the animal, as well as to swerve the course, in the direction of the stimulating object. As stated above, normal dogfish are often seen going round and round, keeping near the walls, with the body tilted to one side so that the mouth and belly are turned somewhat toward the wall. This is just the position which would be produced by the above reactions, if, on making the turn at a corner, the edge of the snout came slightly in contact with the wall. Sometimes I have been able to see such contacts actually occurring, but the asymmetrical position was often assumed when the wall

was not touched. In this case it might be that the increased pressure or resistance of the water when the fish was moving near the wall could act as a stimulus. Indeed I found that a spurt of water from a pipette could be used instead of a finger stroke as a weak stimulus.

For the benefit of anyone who still inclines to the anthropomorphic interpretation of the behavior of the lower animals it may be added that these reactions occur just as well in the dogfish in which all of the fore brain has been destroyed. Indeed beautiful contact responses were obtained from a blinded, labyrinthless fish in which the brain had been cut through at the level of the anterior margin of the optic lobes.

These reactions are not confined to the lower vertebrates; they are seen also in mammals. Magnus¹⁵⁶ has described righting reactions in the rabbit, which are in their fundamental feature essentially similar to those of the dogfish. The forebrain is removed from a rabbit in which both labyrinths had been previously extirpated. Such an animal is able to raise itself into the characteristic sitting position. When laid down flat on its side it first raises its head; then the asymmetrical position of the neck causes unequal changes in the tonus of the muscles of the legs in such a way that the front part of the body is brought into the sitting posture, and finally the hind limbs come into position. The whole chain of movements necessary to complete this reaction is inaugurated by the movement of the head. The head movement in its turn is excited, as Magnus has shown, by the unsymmetrically distributed contact stimuli, namely, the pressure of the skin of one side of the body upon the floor. For if a weighted board is placed upon the upper side of the trunk,

so as to apply contact stimuli to the upper as well as to the lower side of the body, the head is not lifted. The raising of the head is not interfered with by the presence of the board, which rests on the trunk only, but the excitation does not occur so long as the contact stimuli are approximately symmetrical on the two sides of the body.

2. REACTIONS TO RETINAL STIMULI

WHEN a pigeon is rotated on a turntable, nystagmic movements of the head and of the eyes occur. If the table is turned to the right, the head goes to the left a certain distance and then comes back toward the midline with a jerk. These movements are repeated rhythmically. The eyes make similar compensatory movements to the left, *i.e.*, opposite to the turning of the body, and are quickly jerked back. These movements are also repeated rhythmically and constitute a typical eye-nystagmus. If, now, the table is suddenly stopped, the head and the eyes show an after reaction in a direction the reverse of that which occurred during the rotation; the slow movement is to the right and the quick return to the left.

Ewald⁷⁵ found that in pigeons, after the destruction of both labyrinths, nystagmus occurs during rotation, but no after-nystagmus follows the stopping of the table. He found, furthermore, that if a cylinder of gray paper is placed over the operated pigeon, so that the field of vision rotates with the animal, no nystagmus occurs during the rotation. When the labyrinthless pigeon is rotated with eyes open in the ordinary way a succession of images of the surrounding objects must pass across the retina. The effect of these is to cause the eyes to follow them for a certain distance, then the eyes come

back with a jerk, and the process is repeated over and over. When the cylinder is placed around the bird there is no longer the moving succession of images and, in the absence of the labyrinth, no nystagmus occurs.

If a normal pigeon is covered with the gray cylinder and rotated it exhibits no nystagmus or practically none, during the rotation, but differs from the labyrinthless bird in that a marked after-nystagmus occurs when the rotation stops. These experiments show not only that compensatory motions can be called forth by the movement of images on the retina, but also that the retinal stimulation can modify the effects of the excitations arising in the labyrinth. Ewald explained the influence of the retinal images on the compensatory movements and nystagmus during rotation thus: "When the bird looks at objects which do not move along with it the labyrinth effect is increased; when it looks only at objects which rotate with it the effect of the labyrinth is weakened. In both cases there is the effort to retain for the time a constant visual field." This does not explain, however, the very intense after-effect which occurs when the visual field is rotated along with the bird.

A much clearer instance of the influence of moving retinal images upon the compensatory motions which are excited from the labyrinth has been described by Loeb.¹⁴⁵ He noticed that a horned lizard, *Phrynosoma blainvillii*, when held with its eyes toward a window in a moving car made slow movements of the head in a direction opposite to that of the train. The head was bent to a maximum and then came forward with a jerk. This was repeated regularly in response to the motion of the images of the

telegraph posts and other outside objects. A typical nystagmus was thus produced, but when the animal was turned around so that the objects outside the car could not be seen the nystagmus stopped at once. On the same principle a beautiful example of compensatory movements and nystagmus was obtained by rotating around the animal, which was kept at rest, an endless strip of paper on which were painted heavy vertical lines.

Phrynosoma gives beautiful and characteristic compensatory motions when rotated on the turntable. Moreover, the eyes can be caused to close by merely touching them with the finger, and they remain closed without any additional restraint for a time sufficiently long to permit the performance of the experiments described below. In this way Loeb was able to discriminate between the effect of the moving retinal images and the equilibrium reactions excited through the labyrinth.

When a *Phrynosoma* with eyes closed was rotated slowly on a turntable very little compensatory movement of the head occurred during rotation, but when the turntable was stopped a marked compensatory motion was produced. When the animal was rotated with the eyes open vigorous compensatory movements were made during the rotation but the after-effect was very slight. These and other observations enabled Loeb¹⁴⁶ to reach the following conclusions:

“When the eyes of the animal are closed we are dealing only with the geotropic effect of passive rotation; when the eyes are open the orienting influence of the moving retinal image is added algebraically to the orienting effect of centrifugal force upon the ear. These two influ-

ences act in the same sense *during* rotation and therefore are additive; while *after* the rotation they act in the opposite sense to each other.”

Trendelenburg and Kühn²³³ working with another lizard, *Lacerta agilis*, were able to show the effect of moving retinal images in exciting compensatory movements and nystagmus during rotation, but failed to find any after-effects from the retina. They obtained the same result also in the mud turtle, *Emys lutaria*. When one of these animals, in which the right labyrinth had been destroyed, was placed on the turntable and rotated to the right, no compensatory movement occurred during the rotation if the eyes were closed; but when the turning was suddenly stopped a compensatory movement followed. If the animal was rotated to the left with eyes closed compensatory movements occurred during the rotation, but the after-effect was absent. When such an animal was rotated to the right with the eyes open, compensatory movements occurred during the rotation and a compensatory after-effect also occurred; rotation to the left with the eyes open caused compensatory movements during the rotation but the after-effect was absent.

A comparison of these results would suggest the following conclusions: (1) Each labyrinth functions only for rotational movements in one direction; the compensatory movements to the left during rotation to the right are excited from the right labyrinth only, and the after-effects (compensation to the right), are caused by the left labyrinth. (2) Compensatory movements during rotation are excited both through the eye and the ear. (3) The labyrinth gives rise to an after-effect when the rotation stops, but the retina does not.

The last of the above conclusions is hard to reconcile with the very marked after-effect seen in *Phrynosoma*. It is possible, however, that Trendelenburg and Kühn could easily have overlooked a retinal after-effect for the reason that the after-effect of retinal stimulation is in the same direction as the compensation during rotation, and would only be perceived as a prolongation of the compensatory position for a short time after the rotation ceased.

Many other examples of equilibrium reactions from retinal stimulation might be given but the above will serve to indicate the need to discriminate between retinal and labyrinthine effects in research on the functions of the inner ear.

3. REFLEXES FROM MUSCLES AND JOINTS

ANOTHER sort of compensatory movement which can complicate the investigation of the equilibrium reactions, was described by Lyon.¹⁵⁰ In his account he states:

“It occurred to me that bending the body might have some effect upon compensatory motions. I therefore held the head [of a dogfish] (and consequently the semi-circular canals which are supposed to be dynamically stimulated), and bent the tail to one side. The eyes turned as promptly as compass needles. The same day Mr. Garrey pointed out to me that a normal dogfish lying bent and at rest on the bottom of the aquarium always held the two eyes differently. Upon the convex side of the animal the white was more visible in front; on the concave side behind.”

When the tail is bent to the right, so that the body is concave to the right, the two eyes make a conjugate move-

ment to the left. This position is retained so long as the bending continues. The reaction takes place just the same after both optic and both auditory nerves have been cut. An analogous observation had been made by Ewald on the dog. The dog is tied on the table with the head left free. If one now bends the head strongly to the left and holds it there one feels the effort made by the dog to turn the head back to the normal position and one sees at the same time that the eyes are turned strongly to the right. As soon, however, as the dog ceases the attempt to overcome the forced position, the eyes come back to the primary position or at least are moved about freely. If this statement is wholly correct the reaction of the dog differs from that of the fish in that, in the latter, the forced position of the eyes is maintained during the whole time of the bending, while in the former it occurs only while voluntary efforts are made to bring the head back to the normal position.

A reaction like that of the dogfish is also seen in the rabbit. This was discovered by Bárány,¹⁴ who apparently did not know of Lyon's observations. If the head of a rabbit is fixed in a holder so that no motion of the labyrinth can occur to give rise to a reflex, turning the body to one side until the head and body make an angle of 90 degrees with each other, causes a definite conjugate deviation of the eyes to the opposite side. When the body is bent to the right the eyes go to the left, *i.e.*, the right eye turns forward toward the nose, the left eye backward toward the ear. During the bending the eyes move to a point of extreme deviation, then jerk back toward the primary position, again move to extreme deviation and

jerk back. This is repeated usually about two or three times in the turning of the body to an angle of 90 degrees. It thus constitutes a characteristic nystagmus with the slow movement in the direction opposite to the turning. If the body is held at an angle the eyes remain in a forced position. This reaction of the rabbit differs from that of the dogfish only in the occurrence of the nystagmic movements. Of course if the body is fixed and the head is moved to one side the same thing happens, but in that case the labyrinths are also affected by the change of position. This reaction can also be obtained in a rabbit in which both labyrinths have been extirpated. If the body is placed at an angle to the head in some other direction than the horizontal, compensatory eye movements take place in a different plane. All of these compensatory movements are of such nature and direction that they would correspond to and reënforce the reflexes from the labyrinth in the normal activities of the organism.

De Kleijn¹¹¹ confirmed the existence of these reactions in rabbits with both labyrinths destroyed. When in such rabbits he sectioned the dorsal roots of the first and second cervical nerves the reaction could no longer be obtained. This proves that the eye movements in question are excited through afferent impulses from the neck region, presumably through the effects of changes of pressure or tension upon the nerve endings.

It must be remembered that the impulses arising in the neck region affect the tonus of the muscles of the limbs. When, for example, a normal rabbit is laid upon its side, the geotropic impulses from the labyrinth tend to cause the head to be brought up into a position of

symmetry with reference to the vertical. At the same time contact stimuli from the skin of the side on which the body rests, tend also to cause the head to be lifted. When the head then changes its position in relation to the trunk, tonus changes are produced in the muscles of the limbs and these coöperate to bring the whole animal into the normal relation to the vertical. We owe to Magnus and his co-workers a wealth of experimental detail in this field.

CHAPTER VI

EXPERIMENTS ON THE SEMICIRCULAR CANALS

THE separate functions of the ampullæ and of the otolith-organs can be investigated only by methods which make it possible to throw either of the two sets of structures out of activity without injury to the other. The hypothesis of Breuer which assigns all the dynamic functions to the semicircular canals and all the static functions to the otoliths can be put to the test of experiment only in this way.

Extirpation experiments are conclusive if, on destruction of a particular part, a particular function is definitely lost. If, on the other hand, the function continues after extirpation of the part, two possibilities remain; either the function was not performed by the part destroyed, or it was performed by more than one structure. We have already seen that the latter condition exists so far as the general functions of equilibrium are concerned; that, in fact, equilibrium reactions can occur through the influence of contact, retinal, and labyrinthine stimuli. It is necessary then to proceed by the method of exclusion in the use of the extirpation method and to confirm the findings by stimulation experiments. In the statement of the results of these investigations it will be more convenient to describe first the effects of stimulation.

1. STIMULATION EXPERIMENTS ON THE SEMICIRCULAR CANALS

THE older experimenters speak of stimulation in so loose a manner that a few introductory remarks seem necessary. Everyone who is interested in the problems of the labyrinth knows that the sensory endings concerned are not distributed along the extent of the semicircular canals but are definitely localized in the cristæ of the ampullæ. When we speak of the stimulation of a canal or of an ampulla we must be understood to mean the stimulation of the sensory endings in the crista. It is not unusual for writers to speak of stimulation of a canal by rotation of the body (or of the head) in the plane of that canal, although it is not possible under the circumstances, to say that no other part of the labyrinth has been stimulated as a result of the movement.

Flourens⁸¹ described the effects of cutting the various canals and stated that injury to a canal caused movements in the plane of that canal. Cyon⁶² first set out to investigate the effect of stimulating each canal individually, but his statements show that he considered the cutting of a canal as the equivalent of the stimulation of its ampulla. He failed to discriminate between the results of stimulation and destruction.

Breuer⁴⁶ was the first to describe with approximate accuracy the effects of stimulation of the individual ampullæ in the pigeon. Electrical stimulation uniformly caused movement in the plane of the canal. The direction of the movement is not always stated with clearness. Mechanical stimulation of the ampullæ gave more definite results. Pressure on the ampulla of a horizontal canal always caused the head to be turned to the opposite side.

On the whole, Breuer's stimulation experiments were a very important contribution to the investigation of the physiology of the labyrinth.

Ewald⁷⁵ by his very ingenious application of the pneumatic hammer to the mechanical stimulation of the single canals confirmed the observation that stimulation of an ampulla causes movement determined by the plane of the canal, or more correctly, that each ampulla causes movement in one definite plane. The additional deductions from his experiments, that endolymph currents in the canals are the cause of the excitation, and that movement of the endolymph in the one direction causes stimulation and in the opposite direction inhibition, are open to criticism.

Before describing in detail the experimental work on the ears of selachians, which are the best animals for this purpose, it will be desirable to review briefly the anatomical arrangements. The statement is generalized and omits the minuter details in which the different orders are more or less unlike in particulars which have no apparent physiological significance.

The membranous labyrinth (Fig. 4) lies in, but by no means fills, a roomy cavity in the skull cartilage, and hence is surrounded by a relatively large quantity of perilymph. The largest portion is the *sacculus*, S; it rests upon the bottom of the vestibular space, and is larger in the posterior part. The sacculus has openings communicating with the utricle, the recessus utriculi, and the posterior semicircular canal, respectively, while the *lagena* may be considered as a small recess from its posterior, ventral portion. The *utricle*, U, is a some-

what cylindrical, rather wide tube which extends upward, backward, and a little inward from the place of entrance of the anterior vertical and the horizontal canals. It lies upon the recessus utriculi and the sacculus, opening into the former by a short, tubular connection, and into the latter by a long, narrow slit. The utriculus receives, at its anterior end, the mouth of the anterior vertical

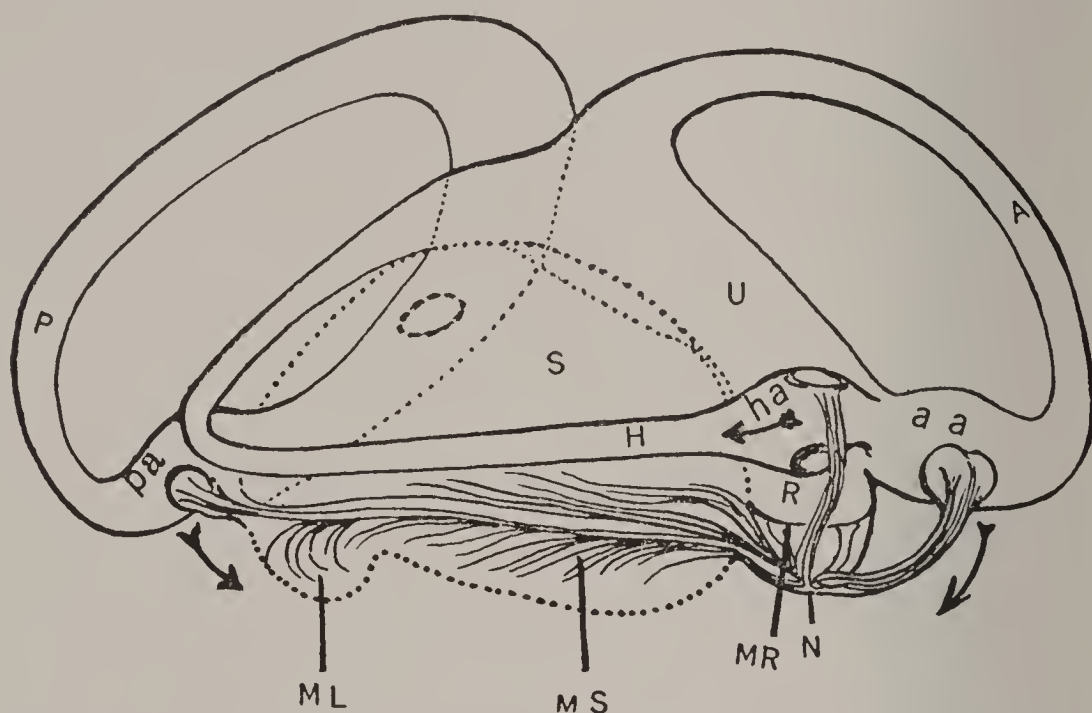


FIG. 4.—Generalized diagram of membranous labyrinth of a Selachian: A, anterior vertical canal; P, posterior vertical canal; H, horizontal canal; aa, pa, ha, the ampullæ of the anterior vertical, posterior vertical and the horizontal canals respectively; U, utriculus; S, sacculus; R, recessus utriculi; MR, macula of the recessus; MS, macula of the sacculus; ML, macula of the lagena; N, eighth nerve sending branches to the maculæ and cristæ.

canal, and just external to this, the mouth of the horizontal canal. Its upper, posterior end corresponds to the sinus superior of other forms, and receives the posterior openings of the anterior vertical and the horizontal canals; it has no direct communication with the posterior vertical canal. The *recessus utriculi*, R, lies below the anterior end of the utriculus. Besides the tubular communication with the utriculus it also has an opening backward into the anterior end of the sacculus.

The three *semicircular canals* stand approximately, but by no means exactly, at right angles with each other. The horizontal, or external, canal, H, is nearly horizontal in its middle part, but its anterior end bends somewhat downward and its posterior part bends strongly upward. The ampulla, *ha*, of this canal is near its anterior end; it opens into the utricle by a short and relatively narrow tube. The ampulla, *aa*, of the anterior vertical canal lies median to and very near the ampulla of the horizontal canal. The anterior vertical canal lies in nearly one plane, at an angle of 35 to 40 degrees with the median plane of the body. The posterior vertical canal, P, forms a ring which has no communication with the rest of the membranous labyrinth except a tubular connection with the sacculus. Its ampulla, *pa*, is in its lower, outer portion.

The branches of the eighth nerve are distributed as follows: to each of the three ampullæ, to the macula of the recessus utriculi, to the maculæ of the sacculus and the lagena, and finally, to the macula neglecta in the wall of the connection between the posterior vertical canal and the sacculus.

The macula, MR, of the recessus utriculi is in a rounded or somewhat oval depression containing the characteristic hair cells, on which rests the lenticular or saucer-shaped otolith of the recessus. The macula, MS, of the sacculus is much more extensive, and that of the lagena, ML, is practically continuous with it. The otolith of the sacculus and lagena is an elongated, flattened mass, very much larger than that of the recessus utriculi. The otoliths consist of calcareous material of a pasty consistency, and can be readily broken up to form a milky

suspension in the ear lymph. The macula neglecta (not shown in the figure) has no otolith.

The cristæ of the ampullæ have hair cells which are not very different in appearance or arrangement from those of the maculæ. Instead of an otolith, however, there rests on each crista a somewhat fibrous appearing gelatinous mass, the cupula, into which the hair cells seem to extend for a short distance. The existence of the cupula seems to be ignored by many writers who speak as if the hair-cells wave freely in the endolymph.

Stimulation experiments on the ampullæ of the dogfish ear have been described by Lee,^{136, 137} Kubo,¹³⁰ and the writer.¹⁶⁹ Lee's account is very closely in accordance with the facts. Kubo used a number of other selachians besides the dogfish. He failed to corroborate Lee in various particulars, but his own work is full of blunders and contradictions.

The ampullæ of the dogfish ear are extremely sensitive to mechanical stimulation. Clear results may also be obtained by electrical stimulation, but the presence of liquids of high conductivity introduces considerable technical difficulty. If the cartilage is carefully sliced away until the ampulla is exposed, the application of light pressure by means of a bristle gives prompt and definite results. Mechanical stimulation may also be obtained by pressing upon the cartilage before the ampulla is quite exposed. If the exposed canal is seized with the forceps and very gently pulled upon the same result is obtained. Experience in these procedures impresses one with the great sensitivity of the ampulla to mechanical stimulation.

Stimulation of the ampulla of a horizontal canal causes a prompt and definite movement of the eyes to the

opposite side. If the right horizontal ampulla is stimulated, both eyes look to the left; or, since the two eyes cannot receive images of the same object at the same time, it would be more exact to say that the two eyes move in a horizontal plane, the right eye going forward toward the nose, the left eye backward toward the gill. The dorsal fins at the same time bend to the left. These it will be remembered are exactly the compensatory movements which are made when the dogfish is rotated to the right around the dorsoventral axis. They are also the eye and fin movements which occur when the fish in swimming turns to the left. Stimulation of the left horizontal ampulla causes the eyes and dorsal fins to turn to the right, the compensatory motions which are produced by rotation to the left in the horizontal plane.

When the ampulla of the right anterior vertical canal is stimulated the right eye is elevated, so that more white shows below the iris, the left eye is depressed, and both eyes roll backward on their axes; the right pectoral fin is depressed and the left pectoral is elevated. These are the movements which occur when the animal is turned head downward to the right in the plane of the anterior vertical canal. When the ampulla of the left anterior vertical canal is stimulated, the eye and fin movements are the same as those which occur when the head is turned downward and to the left, in the plane of the left anterior vertical canal.

When the ampulla of the right posterior vertical canal is stimulated, the right eye goes up and the left eye goes down, as in the case of stimulation of the right anterior vertical ampulla, but both eyes roll forward on their axes. The right pectoral fin turns strongly downward and the

left pectoral slightly upward. These are the reactions which occur when the animal is rotated tail downward and to the right. If the left posterior vertical ampulla is stimulated the reaction may be described by reversing the use of the words "right" and "left" in the preceding part of this paragraph.

It is seen from the foregoing that the statements of Flourens, von Cyon, and others among the older investigators that stimulation of an ampulla causes movements in the plane of its canal, were well founded. The statement, to be accurate, however, should be modified to say that stimulation of an ampulla causes the same movements which are produced by rotation of the animal in the plane of the canal.

Since rotation in the plane of any one of the four vertical canals must be around an oblique axis, or, what is the same thing, simultaneous rotations around two of the axes of reference, it is of interest to note the effect of simultaneous stimulation of two vertical canals. Lee¹³⁸ did this and found that the reaction is the resultant which could have been inferred from the effects of excitation of the two ampullæ separately. Thus stimulation of both the right vertical ampullæ at the same time causes elevation of the right eye and depression of the left eye; but stimulation of each of these ampullæ separately causes this movement, and at the same time a rolling movement which, for each of the two ampullæ, is in opposite directions. It might then be expected that when the two are stimulated simultaneously the rolling motion would be absent, and this is just what happens. The simultaneous stimulation of the two right vertical ampullæ gives the same reaction as that which is produced by

rotation to the right around the longitudinal body axis.

A comparison of the effects of stimulation of the individual ampullæ and the results of rotations around the different body axes leads to the conclusion that the ampullæ contain mechanisms which can give rise to all the compensatory movements; but we can not conclude from this that no other mechanism exists in the ear for the production of these movements. It is necessary first to know what happens in the absence of the ampullæ.

2. EXTIRPATION OF THE AMPULLÆ

MANY of the older investigators appear to have made the assumption that cutting a semicircular canal was the physiological equivalent of the destruction of the canal with its ampulla. It may be stated at once with certainty that this is not the case. In the higher vertebrates the destruction of the ampullæ without injury to other parts of the labyrinth is so difficult while in the fish it is so comparatively easy that we are justified in confining our attention to the results obtained through experiments on fishes.

Lee¹³⁷ destroyed the ampullæ or sectioned the ampullar branches of the eighth nerve in the dogfish. As the outcome of his experiments he arrived at the conclusion that "the section of the nerves of all six canals causes, so far as has been observed, effects similar to those of section of both acoustics, *viz.*, the eyes and fins are normal in position; the fish swims on his belly, back or side, and comes to rest in any one of these positions; after settling on his back or side, he apparently tries to return to his normal position but finds it difficult or impossible to do so; compensation is wanting in all movements."

Lyon^{149, 150} destroyed all the ampullæ or cut their nerves in the dogfish and in flounders and saw, contrary to the results of Lee, the persistence of compensatory movements. According to Lyon, compensatory movements are retained for rotations in all planes after loss of all the ampullæ.

Lee and Lyon each speak of destruction of the ampullæ, but both seem to have relied mainly on section of the nerve branches. By section of the nerve branches, however, they arrived at exactly opposite and fundamentally contradictory results.

After considerable practice I have developed a special technique by which the ampullæ of any or all of the canals may be removed with a minimum of injury and shock to the animal and with results which admit of no uncertainty. A flap of skin is loosened and turned back exposing the appropriate portion of the skull. A thin surface layer of the skull is sliced off with the attachment of some of the neck musculature, thus making visible the parts of the labyrinth through the transparent cranial cartilage. The membranous canal is exposed at a distance not too great from its ampullar enlargement. With a fine pointed pair of curved forceps the membranous canal is grasped as closely as possible to the ampulla and the canal with its ampulla is extracted by a sudden movement, a light quick jerk. Success in this operation depends mainly upon the choice of forceps with the proper curve which bite at the very point, and upon acquiring the knack of removal of the canal by a suitable movement. A too sudden pull will usually break off the canal external to the ampulla, and too slow a movement frequently drags and injures portions of the vestibular structures which it is desired

to leave unharmed. When one has once acquired the knack of this operation the results become absolutely clear. The ampullæ can be extracted one after another with certainty and exactness. In sectioning the nerves one may cut too much or too little; the fibre bundles are scattered, and certainty is impossible. The attempted destruction of the ampullæ *in situ* cannot by any means have the exactness of their complete removal. In many of my earlier experiments I had the ampullæ pasted on a blank leaf of my note book when I wrote down on the same page the results of their extirpation. Under these conditions there can be no doubt as to the correctness of the results. In the summer of 1919, I repeated and extended these experiments at the Marine Biological Laboratory, and on account of the contradictions of previous workers I took occasion to have the experiments witnessed by a number of physiologists and zoölogists.

I previously had found¹⁶⁹ that removal of the ampullæ of the four vertical canals had little or no effect on the compensatory eye movements resulting from the rotation around the longitudinal and transverse axes. In order, however, that there could remain no possible functioning of the semicircular canals I have, in a long series of animals, removed all six ampullæ with uniform results.

A dogfish from which all six ampullæ have been removed shows definitely the following reactions. (1) Compensatory movements of the eyes and fins occur on rotation around a longitudinal axis; *e.g.*, on rotation to the right, the right eye goes up and the left eye goes down. This position of the eyes is retained as long as the abnormal body position is continued. (2) Compensatory movements of eyes and fins occur on rotation around the

transverse axis; *e.g.*, when the animal is tilted head downward the eyes make the characteristic wheel-like backward rotation. (3) Compensation is absent on rotation around the dorsoventral axis. (4) The animal swims in a manner differing but little from the normal. (5) The righting reaction takes place promptly and vigorously; if the animal is placed belly up in water it turns over at once.

As a sample experiment I quote *verbatim* the following from my notes.

"July 14, 1919. Dogfish 5. 10:00 A.M. All six ampullæ removed. Compensatory movements prompt on rotation around longitudinal and transverse axes; none on rotation in horizontal plane. Animal rights itself perfectly in water. Eyelids sewed together to exclude retinal stimuli, and animal put into deep tank; righting perfect.

2:00 P.M. Animal rather weak but rights itself promptly when turned over in water; swims rather wobbly; turned completely over once when excited by other dogfish; I have seen a normal dogfish do this under similar circumstances.

July 15, 9:00 A.M. Animal very weak; rests on bottom of tank in normal position. Rights itself but may swim one or two turns belly up before getting over. Opened stitches in eyelids. No compensatory movements of eyes.

July 16, 9:30 A.M. Animal moribund. Killed for autopsy. Considerable blood clot in each vestibule."

The above experiment shows a possible source of the confusion in the reports of previous investigators. Had I assumed that on account of shock effects, observations made on the day of operation would be unreliable, and had I waited until the following day to make my observations, it would have appeared that loss of the ampullæ abolishes compensatory movements, which is manifestly not true. When immediately following the destruction of an organ a function is clearly retained, it is indisput-

able proof that at least that organ is not the only one which can perform the function. Observation made on July 15, on Dogfish 5, might have favored the statement that destruction of the ampullæ of the semicircular canals abolishes compensatory movements of the eyes, but the observations of July 14 clearly show such a conclusion to be wrong.

In the attempts to determine the rôle of the various sense organs in the geotropic reactions of the dogfish, it has long been recognized that retinal stimuli play a part. Lyon¹⁴⁹ excluded visual stimuli by section of the optic nerve. I accomplished the same result by the less radical operation of sewing the eyelids together, when equilibrium and the righting reactions were under consideration, and by placing a black, opaque disk on the cornea over the region of the pupil when eye movements were to be studied. Other methods of blinding were also used. I can affirm with complete assurance that the compensatory motions described in the case of animals from which all the ampullæ have been removed occur also when activity of the retina has been excluded.

It has been noted that the dogfish, like most animals which rest on the bottom and are not merely suspended in the water, manifests very strong contact reactions. A vigorous specimen which has been blinded and which has had as far as possible all the end organs of the eighth nerve destroyed will almost always be found belly down when at rest. Such a fish may swim indifferently back or belly up, but when it comes to rest the position is a fair index of the general state of the animal. When an investigator affirms that his specimen came to rest indifferently in any position, he has given good incidental evidence as

to the animal's physical condition. In stating that a dogfish deprived of its six ampullæ makes normal righting reactions I have not been unmindful of these facts, but have taken care to exclude the possibility of contact stimuli.

Although it can be proved that after the loss of all the ampullæ, with exclusion at the same time of retinal and contact stimuli, the dogfish makes normal compensatory movements of the eyes and fins to rotations in all vertical planes, it is necessary to note that there are some differences between this and a normal animal.

The following seem to be fairly constant results: (1) The compensatory movements of the eyes, though prompt, are noticeably slower than in the uninjured animal. Compensatory movements due to visual stimuli alone are so much slower, requiring several seconds or even minutes, that no difficulty is experienced in distinguishing these from reflexes of labyrinthine origin. (2) If seized while in the water the animal strongly resists the attempt to turn it back downward. One feels, however, that the resistance is neither so prompt nor so strong as in a normal animal. (3) In swimming there is more or less evident a slight tendency to sway from side to side around the longitudinal axis, like a boat insufficiently ballasted.

These three conditions are less noticeable in vigorous specimens; they become very marked in weakened individuals. They can perhaps all be accounted for by a general lowering of muscle tonus. It is important to note that, as I shall show later, precisely the same complex of conditions can be brought about through a totally different operation.

It may be added for the sake of completeness that the compensatory movements which remain after removal of all the ampullæ are in the blinded animal completely abolished by destruction of the remaining parts of the labyrinth if contact stimuli are excluded.

The foregoing statements apply to the results of the removal of all the ampullæ; it is necessary also to note the effect of destruction of the three ampullæ of one ear. It has been stated by Lee and others that the effect of this operation is practically the same as that of total destruction of one labyrinth or section of one eighth nerve. The animal swims about making turns either to the right or to the left, and does not seem to be greatly inconvenienced. There is a very noticeable forced position of the body, a curving to the operated side, and also a forced position of the eyes and fins; the animal swims with the body inclined to the operated side. If the ampullæ have been removed from the right ear, the right eye is depressed and the left eye is elevated, while the right paired fins are elevated and the left are depressed. The animal makes good compensatory movements to rotations in both directions around the longitudinal and transverse axes. When the fish is rotated around the dorsoventral axis to the sound side, the normal compensatory motion occurs, the two eyes go to the operated side; when, on the contrary, the rotation is to the operated side no compensatory movement follows.

Since, as we have seen, the compensatory movements which are excited by rotation in the horizontal plane are the only ones lost after removal of all the ampullæ, and since stimulation of the horizontal ampullæ causes just these movements, it is of importance to note the effect

of destruction of the horizontal ampullæ alone. When only one horizontal ampulla has been removed rotation to the operated side has no noticeable effect, but rotation to the sound side gives the normal compensatory movement. I have repeated this observation a very great number of times, because it has, as we shall see, an important bearing on the question of the mechanism of normal excitation.

It is possible that the effect of destruction of the horizontal ampulla is not the same in all vertebrates. Ewald found that after complete destruction of one labyrinth of the pigeon compensatory motions are still made to rotations in both directions. Dreyfuss⁷² states that the same is true of the guineapig, although he describes in the same paper the following interesting experiment: Three guineapigs, one of them normal, one with the right labyrinth destroyed, and one with both labyrinths destroyed, are placed in a cage on a turntable and supplied with food. If, while they are all quietly feeding, the table is rotated in either direction, the normal guineapig ceases feeding at once, but the one with both labyrinths extirpated continues eating and pays no attention to the rotation. The one with the right labyrinth removed continues to eat when rotated to the right but ceases at once when rotation to the left begins.

In view of the clear results which one gets with the dogfish, it seems possible that the feeding experiment of Dreyfuss indicates the real labyrinthine effect, and that the nystagmus which he observed on rotation to the operated side was a retinal reaction. Trendelenburg and Kühn²³³ found in the lizard, snake, and turtle, after destruction of one labyrinth, normal compensatory move-

ments on rotation to the sound side, but no reaction on rotation to the operated side if retinal effects were excluded. Ewald's and Dreyfuss' experiments ought to be repeated.

All the evidence seems to show that reaction to rotation in the horizontal plane is the exclusive function of the horizontal ampullæ, and that, clearly in the dogfish, and apparently in many other forms, each ampulla functions only for rotations to its own side, *i.e.*, the right horizontal ampulla responds only to a turning to the right and the left horizontal ampulla to a turning to the left.

A comparison of the results of stimulation and extirpation experiments on the ampullæ of the semicircular canals in the dogfish leads to the following conclusions: (1) All the compensatory movements can be produced through the excitation of the ampullæ. (2) All the compensatory movements except those in response to rotation in the horizontal plane can, in the absence of the ampullæ, be brought about through the action of some other part of the labyrinth.

CHAPTER VII

EXPERIMENTS ON THE OTOLITHS

THE semicircular canals are found only in vertebrates and nothing closely analogous to them occurs in any of the invertebrates. The otolith-organ, on the contrary, is possessed by very many and widely separated orders of invertebrates. A typical otolith-organ consists of a cavity, the otocyst, some part of which is lined with hair-cells, corresponding to the macula of the vertebrate ear, and containing otoliths, or ear sand, resting upon the hair-cells. The otoliths in most animals are deposits or concretions of calcareous matter precipitated from the body fluids; but in certain crustacea, the macruran decapods, the cavity is open to the exterior and the otoliths consists of grains of sand which the animal picks up with its forceps and places in the cavity. In many other invertebrates, of which the brachyuran decapods are examples, well developed otocysts occur which contain no otolithic material.

The experiments of Delage,⁷¹ Kreidl,¹²⁷ Verworn,²³⁶ and others have proved that the invertebrate otocyst possesses, at least in many instances, distinct equilibrial functions. When we put a crab or a crayfish on its back it promptly rights itself. This could be, of course, purely a contact reaction, but the same thing happens if the animal is swimming out of reach of solids. If we destroy the otocysts in one of these animals it still rights itself but less accurately and promptly than before; and if, in addition, the eyes are covered with asphalt varnish so

as to exclude retinal stimulation complete disorientation occurs in swimming.

If the crab or crayfish is moved out of its normal relation to the vertical, *e.g.*, if it is turned a few degrees around its longitudinal body axis, the eyestalks make a compensatory movement as if to retain their original or usual position in space. If the animal is held in the new position the compensatory position of the eyestalks is maintained. This reaction occurs also in a specimen which has been blinded by painting the eyes with black varnish but it disappears when, in addition, the otocysts are removed. These experiments are often taken to support the hypothesis of Breuer that in the vertebrate ear the maculæ with their otoliths are the organs for the static reactions of the labyrinth, while the dynamic functions are performed by the semicircular canals only. This reasoning is faulty, because the reaction of the invertebrate is both dynamic and static; a compensatory movement occurs during the rotation of the animal (dynamic function), and the new pose of the eyestalks is retained so long as the animal is kept in the forced position (static function). Indeed it is hard to conceive of an organ having static functions without having at the same time dynamic functions, although the reverse is quite possible.

The analogy between the otocysts of the invertebrates and the otolith-organ of the vertebrate ear loses force also from the fact, brought out by the work of Clark⁶¹ that the otocysts of *Gelasimus* and *Platyonichus*, which are without otoliths, seem to possess the same static functions as the otocysts of other macrurans do in which an otolith is present. It is plain that we cannot, by experiments

on the otocysts of invertebrates, arrive at definite conclusions in regard to the functions of the otoliths of vertebrates.

Experiments on the otoliths of the vertebrate ear are much more difficult than experiments on the ampullæ. It is indeed a very simple matter to expose and stimulate or remove the ampullæ with practically no harm to the otoliths; but even in fishes, removal of the otoliths without injury to the connections essential to the functions of the ampullæ is far from easy, and in the higher vertebrates it was wholly impossible until Magnus and de Kleijn were able very recently to apply the centrifugalization method of Wittmaack which will be discussed later.

1. EXTIRPATION OF THE OTOLITHS

LOEB,¹⁴⁴ removed the otoliths from the ear of the dogfish both by scratching them out and by washing them out with a stream of water from a fine pipette. By the former method he obtained results comparable to those which follow section of the eighth nerve. When he used the latter method his experiments were a success, for compensatory motions were not lost. Kreidl⁹² repeated these experiments. He stated that dogfish from which the otoliths of both ears had been removed often swam belly up; they came to rest indifferently in any position on the bottom of the aquarium and allowed themselves to be turned into any orientation in the water.

The effects of removal of the otoliths of the dogfish ear were also described by Lee.¹³⁷ According to his description no forced position of eyes or fins resulted from the loss of all the otoliths. If the fish was turned upon its back, it remained quietly in that attitude, or

swam off, gradually turning over; it often swam upon its side; in coming to rest it often settled upon its back. The compensatory movements were weakened but not abolished; the compensatory position was not retained after the cessation of the movement. Removal of the otoliths from one ear caused all the abnormalities which follow section of one eighth nerve.

Kubo¹³⁰ described experiments on the single otoliths. He stated that after the removal of the saccular otolith on one side the rolling movement of the eyes became very indefinite for the position head upward but was unaffected in the position head downward. From this he inferred that, in the head upward position the saccular otolith sliding backward on account of its weight, gives the stimulus which causes the eyes to roll forward on their axes. When, however, he removed the utricular otolith on one side, the reactions to rotations around the transverse axis, that is, in both the head up and the head down position, were absent or very indefinite. The significance of this observation was altogether overlooked. All of Kubo's results appear to have been colored by his anticipations. The inaccuracy of the whole performance is well instanced by his statement that after removal of both otoliths on one side, no reaction occurred to rotation around the dorsoventral axis to the operated side, but a normal reaction took place when the turning was to the sound side. These reactions do not depend upon the otoliths at all but on the ampullæ of the horizontal canals.

It appears to the writer that the work of all previous experimenters on the otoliths has been vitiated by the failure to realize the importance of an avoidance of injury, not merely to the ampullæ, but to the vestibular con-

nections of the ampullæ. On the other hand the importance of experiments on the otoliths in animals in which all the ampullæ have been extirpated, has not been appreciated. The need of these precautions was kept in mind in the performance of the experiments about to be described.¹⁷¹

In the dogfish the otoliths are of soft, friable, calcareous material. In the sacculus there is a large otolith spread over the main macula acustica and a smaller mass on the lagena. These are so situated that their removal can be accomplished with little injury and the operation is relatively easy. For the otolith of the utricle the case is very different. This otolith lies in the recessus utriculi so close to the openings of the ampullæ of the anterior vertical and the horizontal canals that it requires some skill and much practice to remove it without injury to the ampullæ. If, however, after opening the vestibule by removing a portion of the cartilaginous roof, the utricular wall is slit open with a very sharp microdissection knife, the otolith material may be washed out by the careful use of a fine pointed pipette. In a similar way the saccule may be slit open and its otoliths removed. No operation was considered successful unless it was found at postmortem examination that no otolith material remained. For reasons to be stated in another chapter it was considered important not only to avoid injury of the ampullæ but also to reduce the injury of the utricle to a minimum.

After removal of all the otoliths from both ears in successful cases the following results are seen: (1) Compensatory movements of the eyes are made in the regular way to rotations about all three body axes, longitudinal,

transverse, and dorsoventral. If the animal is rotated around a longitudinal or transverse axis and held in the abnormal position the compensatory position of the eyes is retained, but when the rotation is around the dorsoventral axis the eyes make the compensatory movement and then return to the primary position. These movements appear to differ from those in the normal animal only in being slightly slower. (2) The animal swims in normal orientation and maintains its equilibrium in the water, but its swimming, like that of the fish without ampullæ, is likely to be accompanied by a rocking movement; this rocking or swaying is less apparent in vigorous specimens. (3) If turned belly up in the water, the fish rights itself promptly; in doing so, however, it sometimes overcompensates and turns almost or completely over.

It will be seen that these results are strikingly similar to those produced by loss of the ampullæ. It is especially noticeable that there is the same apparent slight slowing of the reactions and the same indication of lowering of muscle tonus in general. In one important respect, however, the result of this operation differs from that of removal of the ampullæ, namely, the compensatory movement to rotation about the dorsoventral axis still occurs. In these observations due care was taken to eliminate retinal and contact reactions.

Parker¹⁹¹ removed the saccular otolith by way of an opening in the roof of the mouth. He found that the loss of this otolith alone produced no noticeable effect on the equilibrium or righting reactions of the dogfish, nor did there appear to be any loss of tonus. I have removed this otolith many times by the method described above. Its loss does not alter or weaken any of the compensatory

movements; it does not disturb the equilibrium or the righting reaction, nor is the muscle tonus affected in any noticeable degree. These results are in conformity with the findings of Laudenbach¹³³ in his experiments on the frog and on *Siredon pisciformes*. Except for a transitory effect of the operation these animals show no disturbance of movement or position after destruction of the saccular otolith.

If the utricular otoliths have been successfully removed and the condition described above has been attained, namely the retention of compensatory movements to rotations in all planes, the righting reaction, and the maintenance of equilibrium, the consequent removal of the six ampullæ produces at once a profound alteration. The condition of a dogfish deprived of the utricular otoliths and the six ampullæ may be stated in the following way: (1) No compensatory movements are made on rotation around any axis whatever. This statement may be modified by saying that in some cases a slow and slight tendency to compensation, requiring many seconds or even minutes for its completion, may be seen. No one familiar with the reactions of the animal would ever confuse this with a labyrinthine reflex. (2) The animal shows no tendency to maintain bodily equilibrium; it swims indifferently back or belly upward. A weak specimen may also come to rest on its side or back, but a vigorous specimen usually rights itself on the bottom of the tank. In other words the geotropic reactions of the animal are definitely and completely lost; the stereotropic reaction is retained.

The results of these experiments show that the assumption of a sharp differentiation of functions between the

otolith-bearing, vestibular portions of the labyrinth and the semicircular canals is not justified by the facts. Between the effects of extirpation of the one and of the other set of structures there is more resemblance than contrast. They certainly reënforce each other, for the reactions produced by either one alone are always slower and less vigorous than when both sets of organs are intact. It would not, however, be safe to affirm that the functions are identical. In one respect a difference is apparent; namely, in the response to rotation in a horizontal plane. Another difference is seen in the effects of removal of all the otoliths or of all the ampullæ from one ear.

Removal of the otoliths of one ear causes very little abnormality of position or movement. It would not be safe to say that no abnormality is produced; but it always seemed that an asymmetry of eyes and fins was only decidedly noticeable in those operations which had not gone smoothly, and where considerable accessory damage had been done to the saccule and utricle. If we place in the same aquarium a dogfish which has had all the otoliths removed from one ear and another which has had all the ampullæ removed from one ear the difference in position will be very noticeable. The fish with ampullæ extirpated will have definite forced positions of body, eyes and fins; the one with otoliths removed will be almost normal in position and movement.

Experiments on the otoliths in forms other than selachians are not very numerous. Lyon¹⁴⁹ reported the removal of the otoliths from the ears of the flounder, *Pseudopleurinctes*, and found that the compensatory movements and the retained compensatory positions were still produced by rotational changes of position. In these

experiments, to exclude the effects of retinal stimulation, he took the precaution to cut both optic nerves. It appears, however, from his statement that he removed only the large otoliths of the sacculi, which Parker and the writer had each found not to be concerned in equilibrium reactions of the dogfish, while he left untouched the really important, though much smaller, otoliths of the utriculi.

Benjamins³² removed the otoliths from the labyrinth in two other bony fishes, namely the perch and the carp. He states that the removal of the saccular otolith causes a decrease in the rotation of the eyes on their visual axes, especially when the anterior pole moves ventrally, the reaction which occurs when the head is tilted upward; there is also an effect, but less in amount, on the reactions to rotation in the other planes. Removal of the utricular otoliths also caused a reduction in the rotation of the eyes on their visual axes, especially when their anterior poles move dorsally, but the reactions to rotations in other planes were almost or entirely lost. If destruction of the utricular otolith causes the loss of reaction to rotations around the transverse and the longitudinal body axes, as Benjamin's experiments seem to show, the condition is the same as in the dogfish; but it is not then clear why removal of the saccular otoliths also had an effect on rotation around the transverse axis. Unfortunately Benjamins did not make clear what amount of incidental injury his method of removal of the saccular otolith may have done to the ampullæ.

The anatomical arrangements in the mammalian ear have, until recently, made experiments on the otoliths seem impossible. A very important contribution to this difficult subject has been made by deKleijn and Magnus.¹²⁰

Wittmaack²⁴⁵ had found that when guineapigs were subjected to centrifugalization at about the rate of two thousand revolutions per minute destructive changes took place in the otolith-bearing parts of the labyrinth, while the cristæ of the ampullæ remained normal in their histological structure. DeKleijn and Magnus made use of the same method, rotating the animals under ether narcosis at a rate of from 960 to 1000 revolutions per minute for from 1½ to 2 minutes. The animals were afterwards carefully tested for their physiological reactions. They were later killed and the histological changes in the labyrinth were studied and correlated with the physiological effect which had been observed. The results of these experiments lead to conclusions which differ in part from those which had been reached by the writer from experiments on the dogfish.

Some of the centrifugalized guineapigs gave normal complementary movements in response to rotations in all planes, but the positions were not sustained after the rotation ceased; in other words, the dynamic functions remained normal but the static functions were lost. The histological examination in these cases showed that the otolith membrane had been thrown out of position, but that the cristæ of the ampullæ remained uninjured. These results of deKleijn and Magnus give strong support to the belief that the ampullæ and the otolith-organs have separable functions; that the ampullæ indeed respond only to movement, and that the otolith-organs on the other hand, are the source of the reflexes of position. It may be that a process of differentiation has taken place in the development of the mammal so that a greater difference exists in the functions of these parts of the labyrinth in

the mammals than in the lower vertebrates. The results of further investigation of this question will be a matter of great interest.

2. STIMULATION EXPERIMENTS ON THE OTOLITH-ORGAN

DIRECT stimulation of the otolith-organs are not very easy to perform even in selachians, which, on account of the large size of the vestibule, are the most favorable animals for the purpose. In these fishes, however, the friable nature of the otoliths makes it difficult to apply mechanical stimulation without immediate injury; a very little pressure causes them to break up and renders the results uncertain. Moreover the vestibular parts of the membranous labyrinth which overlies the otoliths are connected directly with the mouths of the semicircular canals very near to the ampullæ. On account of the high sensitivity of the ampullæ to mechanical stimulation, the attempt to reach and stimulate the otolith-organs without previous removal of the ampullæ is almost certain to give confused and unreliable results.

Lee¹³⁷ reported the effects of stimulation of the maculæ to be exceedingly variable. The stimulation brought forth in the same animal at different times, the same eye and fin movements as those which follow the stimulation of the three ampullæ. Since Lee does not mention that in any of these experiments he had previously removed the ampullæ, the presumption is strong that some at least of his results were really caused by the excitation of the cristæ instead of the maculæ.

Kubo¹³⁰ described experiments on the otoliths in a number of dogfish, skates, and rays with results which accorded very nicely with the hypothesis of Breuer that

the vestibule has three otoliths in three planes in space, directly comparable to the semicircular canals; the otolith of the utricle being horizontal, and those of the saccule and lagena vertical and perpendicular to each other. Moreover, according to Breuer, each of these has a groove in which it can slide more readily than in any other direction. This idea of Breuer's seems to have had a fascination for many minds, for it has reappeared in a number of slightly different forms. It has led to some very beautiful anatomical work, but it has not had much support of the most essential kind, namely, from physiological experiment, and the results of stimulation of the utricular otolith have been found by the writer to be completely fatal to the hypothesis.

A working hypothesis clearly formulated and properly used can be of very great service in scientific investigation; but it can also become a source of expectations which, where results are at best difficult to observe and record, may lead one to think he sees exactly those things which justify his expectations. This appears to have been the case with Kubo in his experiments on the ears of selachians.

Kubo reported that in the opened vestibule he could see the otoliths slide on account of their weight, when the fish was tilted far enough to cause complementary eye movements. When the head was tilted downward he believed he saw the utricular otolith slide forward; when the head was elevated he thought the saccular otolith moved visibly backward. He also described eye movements resulting from stimulation of the maculae by the application of pressure to the different otoliths. Since Kubo's account of the much simpler experiment of stimu-

lation of the ampullæ is full of mistakes, one cannot feel that his observations on the otoliths are to be taken seriously. It is very evident that he did not remove the ampullæ; indeed he expressly states that the experiment succeeded better when the vestibule was opened and the stimulation performed "without removing the gelatinous capsule." According to Kubo, pushing the otolith of the recessus utriculi forward caused the eyes to roll backward on their axes, *i.e.*, into the compensatory position for the head downward posture of the fish; this we know is the effect of stimulation of the ampulla of the anterior vertical canal. Pushing the same otolith backward had no effect. Pushing the otolith of the sacculus backward caused the eyes to roll forward on their axes, *i.e.*, the reaction for the head up position; pushing the saccular otolith forward had no effect. When he pushed the saccular otolith outward the eye on the stimulated side was elevated. Sometimes, however, he saw eye movements in the horizontal plane when he touched the middle of the saccular or the posterior part of the utricular otolith. Referring to these horizontal movements he says, "In this case one cannot exclude the possibility that the horizontal ampulla was indirectly affected," for it stands in close relation to the utricular otolith. The resulting confusion emphasizes the necessity of complete removal of the ampullæ before attempting stimulation experiments on the otoliths.

In my extirpation experiments I had found that after removal of all six ampullæ, and after washing out the large otolithic masses of the sacculi (and lagenæ), the dogfish and the ray still gave good compensatory movements in response to rotations around the longitudinal

and the transverse axes.¹⁷² These responses I proved to be dependent on the presence of the otolith of the recessus utriculi for they disappeared when it was removed. I also found it possible to stimulate mechanically the otolith-organ of the recessus and to get results just as clear and consistent as those obtained from stimulation of the ampullæ. I quote the following record of an experiment.¹⁷³

“ July 16, 1920. Large dogfish (*Galeus*).

Opened both ears and removed all six ampullæ.

Using a stiff bristle tipped with wax and the wax covered by a thin layer of absorbent cotton, applied pressure to various parts.

Right ear.

Pressed on right (lateral) side of otolith (of recessus utriculi); right eye depressed, left eye elevated.

Pressed on left side of otolith; left eye depressed, right eye elevated.

Repeated several times with uniform results. Otolith soon disintegrated: no more response.

Left ear.

Pressed on left side of otolith; left eye depressed, right eye elevated.

Pressed on right side (median) of otolith; right eye down, left eye up.

Repeated several times with same result.”

Experiments made in this way gave fairly constant results, but it was not possible to repeat the observation many times without injury to the otolith-organ. A new and very simple method was later found which permitted repetition of the stimulation many times before serious damage was done to the otolith and which gave absolutely constant results. The experiment is performed as follows:

A small mass of absorbent cotton is formed into a tiny cushion about the size of the otolith of the recessus and

is cautiously placed on top of that otolith. The cotton is then grasped with the points of a fine forceps and gently moved to the right or left, forward or backward at will. I quote again from my notes:

“July 23, 1920. Large shovel-nosed ray (*Rhinobatus*).

Removed ampullæ from left ear.

Exposed small otolith (of recessus utriculi) and placed on it the pellet of cotton.

Movement of pellet to left caused depression of left eye and elevation of right eye.

Movement of pellet to right caused depression of right eye and elevation of left eye.

Movement of pellet forward caused both eyes to roll forward on their axes (anterior pole of each eye depressed and posterior pole elevated).

Movement of pellet backward caused both eyes to roll backward on their axes.

When pellet was moved to one side eyes moved in same sense.

When pellet was held to any side, the eye position was retained.

Removed the three ampullæ of the right ear.

Repeated the experiment on the right ear with exactly the same results.

Repeated a score or more of times with no noticeable diminution of the response.

Holding the pellet to any side held the eyes in the corresponding position.”

I have repeated these experiments on dogfish, leopard sharks, and rays. The experiments on the ray (*Rhinobatus*) were particularly striking. This fish is broad and flat and usually remains at or near the bottom of the water. It is not, apparently, used to much turning over or tilting of the head up or down. Taken out of the water, or rotated in the water it does not show any of the compensatory movements in so marked a degree as does the dogfish. When, however, the stimulation was applied to the recessus as described above, the eye movements were

extraordinarily vigorous, much more so than in response to rotation of the body of the uninjured animal. The eyes rolled right or left, forward or backward, as if on actual mechanical axes manipulated by cords.

These results were at first very surprising. Following the *a priori* reasoning usually applied, I had expected that pressure on the right side of the otolith would have the same effect as inclining the head to the right, for the weight of the otolith ought to cause a pressure on the side to which the head was inclined, and I supposed that this pressure would be the adequate stimulus. I found, on the contrary, that pressure on the *right* side of the otolith of either ear produces the same eye movement which results as the compensatory motion to rotation of the body to the *left* around the longitudinal body axis; and that pressure on the *anterior* side of the otolith gives the same effect as tilting the head *upward*. In each case the response is precisely opposite to that which would be expected if the stimulation were produced by the pressure due to the weight of the otolith; for when the body is tilted to the right, the weight of the otolith must be shifted to the right, but the reaction to this rotation is elevation of the right eye and depression of the left eye. When pressure is applied directly to the right side of the otolith, as in the experiments above described, the opposite result is obtained; namely, depression of the right eye and elevation of the left. It must be, then, that the stimulation does not result from the direct effect of the pressure but from the shifting of the otolith; a displacement to the left is brought about by

pressing on its right side under the conditions of the experiment, and a similar displacement to the left results from tilting the animal to the left. In other words, it is the *displacement* of the otolith, and not the pressure due to the weight of the otolith, which is the actual stimulus and it is the *direction* of the displacement which determines the direction of the compensatory movement in response to the stimulus.

CHAPTER VIII

THE MECHANISM OF THE DYNAMIC FUNCTIONS OF THE LABYRINTH

WE HAVE seen that the ampullæ alone, without the otoliths, suffice for all the dynamic functions of equilibrium of the ear, and that the otolith-organs alone, without the ampullæ, also suffice for all the dynamic functions except that of response to rotation in a horizontal plane. It now remains to consider the mechanism through which these functions are called into play.

1. THE DYNAMIC FUNCTIONS OF THE AMPULLÆ

MACH, Brown and Breuer at first attached paramount importance to the space relations of the semicircular canals. It was assumed that rotation of the head in the plane of a canal caused, by the inertia of the endolymph, a current within the canal contrary to the direction of rotation. It was supposed that the hair-cells of the crista were deflected by the current and stimulation of the nerve endings resulted. Mach,¹⁵¹ however, very soon saw that, under the conditions existing in the labyrinth during normal physiological stimulation, such a current could not be produced, and Breuer⁴⁸ later admitted that the hair-cells do not project into the endolymph but are covered by the gelatinous mass of the cupula.

Mach's later view was that an endolymph movement could not occur in the semicircular canals as the result of a rotational movement of the head, but that a tendency to move would be the result. A tendency to move, without the occurrence of actual motion, can be nothing else than

a pressure. This raises the question whether a pressure of this order of magnitude could really act as a stimulus. That pressure alone is not the stimulus which gives rise to compensatory movements, can be shown in a variety of ways (Lyon,¹⁴⁹ Maxwell¹⁷⁰).

When the horned lizard, *Phrynosoma*, is moved in a straight line with the long axis of its body perpendicular to the direction of the movement, beautiful compensatory motions are made, if the animal's eyes are open. If the direction of movement is to the animal's right the head and eyes turn slowly to the left and then suddenly jerk back to the primary position. This action is repeated rhythmically and constitutes a typical nystagmus with the slow component in the direction opposite to that in which the animal is moved. This nystagmus is excited by motion in a straight line, movement of translation, only while the eyes are open; not a trace of compensation occurs when retinal stimulation is excluded, even if the movement is so sudden and so rapid that the animal must be tied to prevent its being thrown off the board. When a dogfish is moved similarly in a straight line no compensatory movement takes place even if the eyes are open.

A lateral movement of translation must of necessity cause a pressure, through the inertia of the contents of the labyrinth, and yet no compensatory movement is excited. If, however, the movement of the animal deviates from the straight line so that an arc, even of very long radius, is described the compensatory movement is elicited. This observation alone would indicate that not merely pressure, but a movement of rotation, a torsion effect, is a necessary factor in bringing about the excitation.

It has been argued that, in a movement of translation to the right or left, the pressure conditions in the right and in the left labyrinths are in the opposite sense; when the pressure in the right ear is to the median side, the pressure in the left ear is to the lateral side of the cavity. Under these conditions, it has been assumed, the excitations from the two ears would tend to have exactly opposite effects and hence would neutralize each other. But a dogfish in which one labyrinth has been extirpated, and which still shows good compensatory movements when rotated to the sound side, gives no compensatory movement to pure movements of translation either to the right or left.

It has also been argued that pressure changes could not be produced in the ampullæ by any rectilinear movement, because the ampulla and canal form part of a closed ring which must therefore move as a unit. This would be true if the membranous labyrinth were a rigid and not a flexible system, or even if the membranous labyrinth were enclosed in a rigid capsule completely filled with incompressible liquid; but this is not at all the case. In the selachians the perilymphatic space is in communication with the exterior through the ductus endolymphaticus, and also it is not rigidly separated from the cranial cavity. In many of the bony fishes, one or more of the semicircular canals lie free in the pial space of the cranial cavity (Parker,¹⁹² Benjamins³²). De Kleijn and Magnus¹¹⁹ have pointed out that in the mammal, the labyrinth is separated from the tympanic cavity by a partition which is not wholly unyielding, and they have described a model which shows that rectilinear motion can produce

a movement or relative change of pressure in a structure arranged like the ampullæ and canals.

We are not discussing here the question of the existence of sensations or reflexes excited by movements of translation and mediated through the labyrinth. The observations of Ach,¹ and of deKleijn and Magnus¹¹⁹ make it evident that such reflexes exist; but the responses are not such as could be mistaken for the compensatory movements with which we are at present concerned.

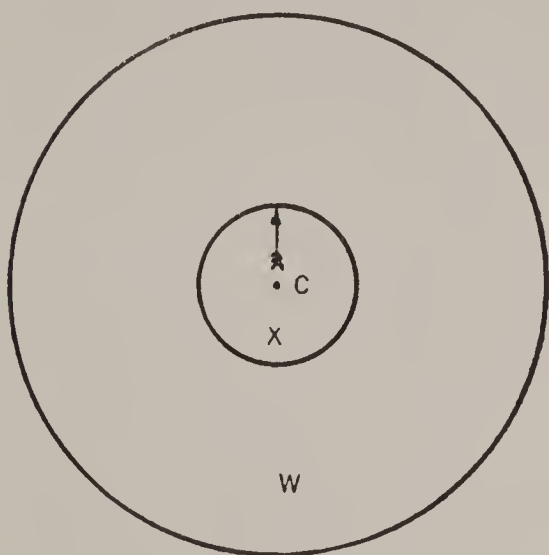


FIG. 5.

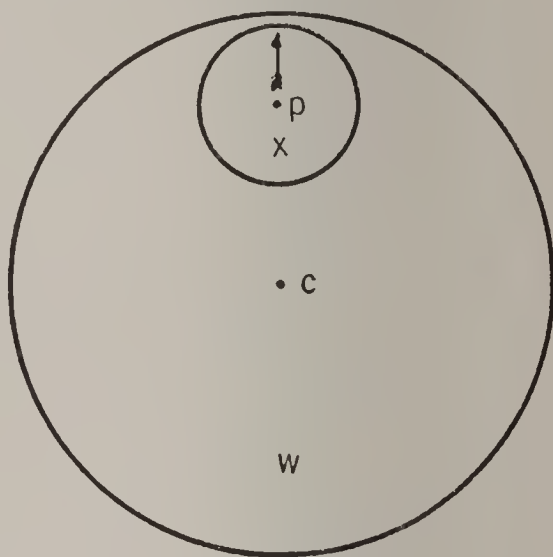


FIG. 6.

Since, then, the compensatory motions are elicited by rotational movements only, we must analyze more closely the forces which bring about the excitation. Imagine a wheel *W* (Fig. 5.) with another wheel *X* mounted upon it, so that the axis of *X* is coincident with the axis of *W*. If the bearing on which *X* is mounted could be absolutely frictionless then the rotation of *W* could have no effect on the orientation of *X*; the arrow upon *X* would continue to point in its original direction. If now the axis of *X* be connected to the wheel *W* by a wire which is rigidly attached to both wheels, the rotation of *W* will tend to be

communicated to X , but the inertia of X will oppose this tendency, and the wire will be subjected to a certain amount or torsion before the angular velocity of X becomes equal to that of W . We may call this part of the effect of the inertia of X its *torsion effect*.

If we next move the wheel X to some eccentric position, as at P (Fig. 6.) and if the mounting of X is frictionless the rotation of W will not cause a change in the orientation of X ; if the arrow was directed to the north at the beginning it will continue to point north during the rotation of W . But if we suppose once more the axis of X to be connected to the wheel W , then, as before, when W is rotated the inertia of X will exert a torsion effect upon the connecting wire. The amount of this torsion will be the same in the two cases.

But in the eccentric position of X another inertia factor will have to be considered, namely, the *centrifugal force*, which is the pressure exerted at P along the radius CP . For any given rate of rotation the amount of this pressure varies directly as the radius of the circle described by P around C , and for any given radius the pressure varies as the square of the angular velocity; or, stated in general terms, $F=mrW^2$ where F is the centrifugal force, m the mass of the rotating body, and W the angular velocity.

In the equilibrial reactions of the labyrinth we have to distinguish between the possible centrifugal effect and the torsion effect. This was investigated in the following way.¹⁷⁰

An animal was placed on a turntable and slowly rotated through an angle of 45 degrees. By a series of trials a rate of rotation—to be more exact, an accelera-

tion—was found which was just equal to the threshold of stimulation. The animal was then placed at some other distance from the axis of rotation and the threshold again determined. The radial force for any given particle of a rotating body, at a given rate of rotation, varies as the distance of that particle from its centre of rotation. The torsion effect, on the other hand, depends on the angular velocity, but not at all on the radius. If it can be shown that a position on the turntable at a distance from the axis is more effective in evoking the compensatory movements than a position nearer to the centre, then there is evidence that pressure is an effective stimulus. If no such difference exists, the exciting cause must be the torsion effect alone.

The animal used was the horned lizard, *Phrynosoma*, commonly known as the horned toad. This is especially convenient for such experiments as Loeb¹⁴⁵ had pointed out, because of the fact that the eyes can be caused to close by merely touching the lids, and retinal reflexes are thus very simply excluded. To facilitate the observation of very weak reactions a light straw, as index, was attached to the animal's head and projected 80 mm. beyond the snout. A graduated arc was marked on the turntable, and in this way very slight movements could be perceived. Table II. shows a specimen experiment. The turntable was rotated by hand through an arc of 45 degrees in each case; the time occupied in that amount of turning was indicated by a stop watch and is set down in column 2. Several trials were made in the one position; then the animal was moved to the other position and a number of trials made. This was done to eliminate pos-

sible changes in the excitability due to the effect of handling. The order of the trials is indicated by the trial number in column 1. The response is shown in column 3.

TABLE II.

EFFECT OF ROTATION THROUGH 45 DEGREES AROUND A VERTICAL AXIS.

Head 25 mm. from centre of turntable			Head 300 mm. from centre of turntable		
1 Trial No.	2 Seconds	3 Compensatory movement	1 Trial No.	2 Seconds	3 Compensatory movement
1	7	Slight	6	8	Slight
2	7	Slight	7	9	None
3	12	None	8	9	Slight
4	10	None	9	10	None
5	8	Slight	10	10	None
14	8	Slight	11	8	Slight
15	8	Slight	12	7	Slight
16	8	Slight	13	6	Strong
17	6	Strong	22	10	None
18	5	Strong	23	9	None
19	10	None	24	8	None
20	9	None	25	7	Slight
21	7	Slight	26	5	Strong

A second set of observations was made in which the animal was placed upon a board which could be rotated smoothly through 45 degrees about a horizontal axis.

Inspection of Table II. shows that the threshold for horizontal rotation was reached with a speed of about 8 seconds for 45 degrees and that there is practically no difference in the effect produced when the distance from the centre is altered. A similar result was obtained for rotation around the transverse axis of the body. Since increasing the centrifugal force twelve fold has no appreciable effect on the threshold of stimulation we are

justified in concluding that in rotational movements, within ordinary physiological limits, the influence of centrifugal force is negligible, and that the excitation depends wholly upon the torsion effect.

It is also significant that the direction of the torsion determines the sense of the compensation. This is shown by the following well-known fact: When an animal is placed in an eccentric position on the turntable and is rotated to the left (the observer's left) the compensatory movement is to the animal's right whether the head is directed toward the circumference or toward the centre. But when the head is directed to the circumference the compensatory movement is opposite to the movement of the animal as a whole; when the head is directed to the centre the compensatory movement is in the same direction as the movement of the animal. This is illustrated by the accompanying photograph (Fig. 7).

The semicircular canals have been commonly believed to be an essential part of the mechanism for the normal excitation of the ampullæ. Nevertheless direct experiments show that the ampullæ are not necessarily dependent on the canals for the performance of their functions. It was found by Loeb¹⁴³ that in the dogfish the canals could be cut through and even large portions could be excised without affecting the compensatory movements or the functions of equilibration, and Ewald's experiments indicated that, in the pigeon, after the canals had been ligatured, plugged, or cut, compensatory movements of the eyeballs and eye nystagmus were produced by rotation.



FIG. 7.—Compensatory position of frogs photographed while rotating to left. The center of the dish containing the frogs was about 16 inches from the center of the turntable. The frog on the left faced the center, the one on the right the periphery.

These experiments show that the canals are not necessary to the dynamic functions. Certain objections, however, might be raised. Loeb does not state specifically that all the canals were cut. Since I have shown that all the dynamic functions except that of response to rotation in a horizontal plane may be performed by an ear from which all the ampullæ have been removed, it would be necessary to know that the horizontal canals had been cut before the proof could be considered complete. Furthermore, in the dogfish each horizontal ampulla reacts to rotations in one direction only; this according to Ewald is not the case in the pigeon but his proof of this is also incomplete.

Since, in the dogfish, the response to horizontal rotation is brought about by the horizontal ampulla only, it would be a crucial experiment artificially to change the plane of this canal with reference to the skull of the animal and see whether this change does or does not alter the response to rotation. I have succeeded in doing this by the following method.¹⁷²

The right horizontal canal was laid bare for nearly the whole distance from its ampulla to the point where its posterior end reënters the vestibule. It was then ligatured and cut as far posterior as possible and the cut end was gently lifted into a vertical position, laid over against the skull, and supported there by a pledget of cotton. Its new plane was at right angles to its original plane and also at right angles to the long axis of the body. It is needless to say that in this operation extreme care must be taken not to exert the least traction

on the ampulla. It is clear that with the canal in the new position rotation of the animal in a horizontal plane, that is, around a dorsoventral axis, could not even theoretically give rise to a current in the canal. On rotation to the right, however, the eyes turn to the left and on rotation to the left the eyes turn to the right; that is, the ampulla whose canal is now at right angles to its normal position acts just like the other ampulla whose canal is still horizontal. On the other hand, rotation of the animal around its longitudinal axis (in the new plane of the canal) never produces a deviation of the eyes to the left as it might be supposed to do if the rotation causes a current in the canal and the current excites the ampulla. This experiment, then, shows conclusively that the excitation of the sensory structures in the ampulla is due to some other cause than the production of a current in the canal.

The experiments just described show clearly that the function of the ampulla does not depend primarily on the canal, but that it can be performed under conditions in which it is impossible for a current to exist. It would therefore be of no consequence to consider whether Mach was right or wrong in his conclusion that on account of the small size of a semicircular canal, a movement of rotation could not produce a current but only a momentary impulse. It has been assumed, however, by many writers that proof of the occurrence, or even of the possibility, of a current in the canal, is also proof that the current is the cause of the excitation. It will be of interest then to review briefly some experimental work on this question.

Mach¹⁵¹ constructed a glass model of the form and size of a human semicircular canal.* When this was filled with liquid and rotated on the centrifugal machine no movement of the liquid could be perceived. Rossi²¹⁷ made a collodion model and filled it with a liquid containing suspended particles for the easier observation of movement. When this was rotated a counter movement of the particles was seen. Maier and Lion¹⁶⁵ made similar experiments with capillary glass tubes of different diameters using for endolymph a suspension of blood corpuscles in physiological salt solution. With a compound microscope, objective No. 3, they were able to see a relative movement of liquid in the tube at the beginning and end of rotation. They distinguished the following stages: (1) At the beginning of the rotation the liquid appeared not to move at all. (2) On account of friction the liquid began to move, but more slowly than the tube. (3) The movement of rotation having become uniform, the liquid and the tube moved at the same rate; no relative movement to be seen. (4) When the rotation was stopped the liquid moved onward in the tube for a brief time. With a relatively large tube they found that stage 4, the after-movement, could last 2 to 6 seconds. When, however, they used a tube 0.75 mm. in diameter, therefore

* Most persons who have experimented with models of the semicircular canals have seemed to assume that it would be sufficient to use tubes of the calibre of the canals in the human ear. We must remember, however, that there are animals which seem to exhibit good labyrinth functions, but which possess canals of a very different diameter. According to Gray,⁹² the canals of the squirrel's ear have about one-fifth the diameter, and hence about one twenty-fifth the cross-section, of those in the human ear. These proportions must very greatly decrease the inertia effect of the contents of the canals and at the same time enormously increase the resistance to movement on account of friction.

of a lumen nearer to that of a semicircular canal, stage 4, though still perceptible, was too short to be measured. This remained true after a rotation of twenty seconds or longer. Stages 1 and 2 were also momentary. Similar observations were made on the actual canals of the pigeon and the codfish.

Maier and Lion assume, on the basis of their experiments, that the inertia currents produced in the canals by the rotation of the head are the adequate stimuli for the ampullæ. When a man is turned in a revolving chair, for the first instant, only a fraction of a second, the endolymph, on account of its inertia, remains at rest. The peripheral ends of "the sensory hairs of the cupula," or the cupula itself, are struck against the motionless fluid and are strongly bent in a direction opposite to the revolution. This excites a lively nystagmus. On account of the friction the motion more and more approximates to that of the canal (stage 2). During this time the sense hairs are still bent and continue to send impulses to the central nervous system. This period is extraordinarily short. During the remainder of the rotation endolymph and canal move alike. When the rotation is stopped the endolymph continues to move on account of its inertia, and bends the hair-cells in the direction of the rotation (stage 4).

Maier and Lion realize that the two periods (stages 1 and 4) in which the liquid could be seen to move were each only momentary. The after-movement, stage 4, though perceptible to the eye was too brief for an estimation of duration to be made, yet the after-nystagmus which it is supposed to induce lasts 20 seconds or longer. These authors admit that neither this nor the long lasting ny-

stagmus at the beginning of the rotation, represents the actual time of movement of the endolymph. Indeed, according to their observations and conclusions, an after-nystagmus lasting 20 seconds is excited by an endolymph current lasting a small fraction of a second. For this reason they are led to argue that the sudden bending of the hair-cells gives rise to chemical changes the effect of which continues for some time after the bending has ceased. Such a change, however, can easily be accounted for without assuming an endolymph current in the canal at all. The observations of Maier and Lion do not, as they suppose, prove the endolymph current to be the cause of the excitation of the ampulla; but, on the other hand, they show the absence of any direct relation between current and stimulus.

No further consideration need be given to the possibility of currents in the semicircular canals as the cause of the excitation which, on rotation, gives rise to the reflex compensatory movements. We must therefore consider other possible causes. These might be: (1) effects dependent on the inertia of the mass of liquid or other material in the vestibule, or (2) due to the inertia of the contents of the individual ampullæ, or (3) to inertia effects within the sensory cells themselves. It would be impossible to decide between these *a priori*.

In my earlier experiments I found that after destruction of the structures in the vestibule I could never obtain compensatory movements on rotating the dogfish around its dorsoventral axis. For a long time I was inclined to think that the absence of the reflex was due to some sort of injury to the ampullæ, although these appeared to be as sensitive as before to direct mechanical stimulation;

the slightest pressure caused decided eye movements. When, however, I was finally able to remove the otolith from the recessus utriculi by slitting open the utriculus lengthwise without tearing it across I found that the compensatory movements to rotation in the horizontal plane were not abolished. Since the destruction or the transection of the utriculus abolished the reflex with no apparent reduction in the direct sensitivity of the ampulla it became clear that the utricular (and possibly the saccular) structures are essential parts of the mechanism.

In attempting to analyze more closely the arrangements of the parts concerned, it is to be noticed that the movement of rotation which acts as a stimulus to any given ampulla carries foremost the side of the ampulla which bears the crista. Thus the cristæ of the anterior canals are on the lower side of their ampullæ and a rotation around a transverse axis in the direction head downwards excites them; the cristæ of the posterior canals are also on their lower sides and a rotation around a transverse axis in the direction head upwards (back part of the head downward) excites them. So also the crista of the right horizontal canal is on its right or outer side and the stimulus for it is rotation to the right. Of course a similar relation exists for the left ampullæ. Examination of the extensive series of drawings by Retzius²⁴⁹ shows that the dogfish is not a special case but that the arrangement is general.

A second fact which is significant is that the mouths of the ampullæ are continuous with the utriculus, an elongated, thin walled sac, stretched across the cavity of the vestibule and occupying only a portion, in the dogfish a not relatively large portion, of the vestibular space.

Furthermore the utricle is so attached by means of the sinus superior and other structures that it is relatively free to move toward the dorsal but not toward the ventral side of the cavity. The relations as far as the ampulla of the anterior vertical canal is concerned are shown diagrammatically in Fig. 8. Rotation of the head

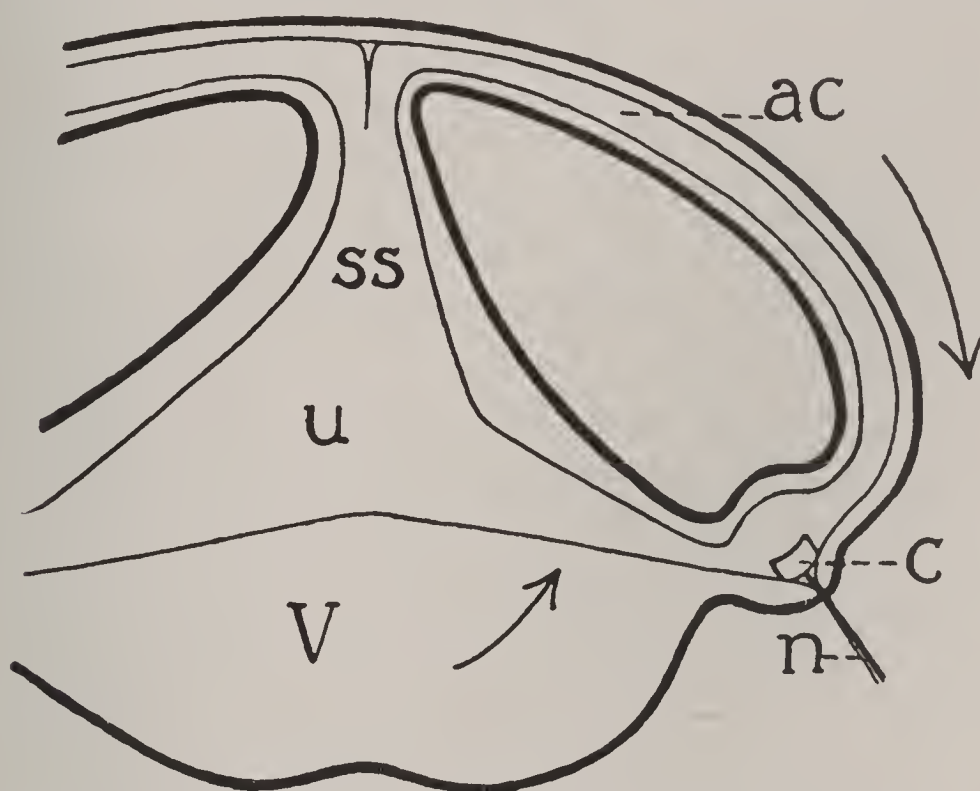


FIG. 8.—Diagram to illustrate relation of vestibular structures to ampulla, v, vestibule; u, utricle; ss, sinus superior; ac, anterior vertical canal; c, crista; n, nerve.

downwards, that is, in the direction of the outer arrow, would tend by inertia, to produce the same effect as if, with the head stationary, the perilymph was rotated in the opposite direction, as indicated by the small arrow within. This would put pressure and tension on the under side of the anterior end of the utricle; this tension would be communicated to the ampulla and especially to its lower side which bears the crista. Rotation in the opposite direction could not exert the same traction on the ampulla.

In order to convince myself of the correctness or incorrectness of the above reasoning, I constructed a model by carving cavities and channels corresponding to the relations shown in Fig. 8. In these I placed a thin rubber model of the two canals shown in the figure. The canals and utriculus as well as the perilymphatic space were filled with mercury. On rotating the apparatus it could be seen that movement in one direction gave a very perceptible pull on the ampulla; movement in the opposite direction was almost without effect. It is possible that the rotation which puts the ampulla under mechanical strain would also tend to produce an increased liquid pressure within it, but this was not investigated.

Careful dissection shows that mechanical relations analogous to those just described hold also for the posterior ampulla and the horizontal ampulla.

I wish to point out the advantage which the vestibular mechanism possesses on account of the mass of liquid. A relatively large free mass of liquid with a relatively small surface would show more inertia effect than a small mass with a relatively large surface area.

This principle was nicely shown by a model made by W. H. Hoyt, a student of mine. The model consisted of a glass tube of approximately 1 mm. lumen, bent into a circle, and having at one place an enlargement of several millimetres diameter to represent an ampulla. The space was filled with a liquid containing minute flakes of aluminum powder. When the model was rotated very rapidly and then suddenly stopped he could, indeed, see some movement for an instant in the canal, but the striking fact was that a marked rotational movement of considerable duration took place in the ampulla. The dimensional

relations of the ampulla in Hoyt's model would more appropriately represent the vestibule. Certainly the larger cavity allows greater opportunity for a longer lasting after-rotation.

It has not been a part of our problem to find explanations for the existence of structures in the labyrinth, but, on the contrary, to find out where and how definite functions are performed. It may be suggested, however, that liquid may move through the canals, not as a stimulus to the nerve endings in the cristæ, but as a means of equalization of pressure. Indeed, if the ampullæ were mere diverticula from the vestibule it is conceivable that pressure conditions could arise in them which might seriously affect the performance of their functions. If these injurious pressures were caused by rotation of the head, then the effective provision for relief would be a circular passage in the plane of the movement which caused the pressure. It is not unreasonable to suppose that the canals supply a means for the equalization of liquid pressure quite analogous to the use of the Eustachian tubes in equalizing air pressure.

The fact that in man and many mammals a nystagmus can be caused by irrigating the auditory canal with hot or cold water and that the character of this nystagmus differs for different positions of the head can be explained perfectly without assuming the action of currents in the canals. If the temperature difference can cause convection currents in the internal ear under the conditions existing in such an experiment, as the work of Maier and Lion seems to make probable, it is certainly reasonable to suppose that the effect would be far greater in the relatively large mass of liquid in the vestibule than in

the much smaller space in the canals. The difference of specific gravity which would be produced in the vestibule would cause changes in tension perfectly consistent in their effects with the tension changes produced by inertia during a movement of rotation. These considerations would not in the least invalidate the diagnostic use which Bárány has made of the phenomenon, but they do supply a reasonable explanation of its causation.

2. THE DYNAMIC FUNCTIONS OF THE OTOLITH-ORGAN

WE HAVE seen that after removal of all the ampullæ from both ears of the dogfish reactions occur to rotations in all planes except the horizontal, and this condition remains unchanged if, in addition, we then remove the sacculus otolith. In other words, compensatory movements to rotations around the longitudinal and transverse axes continue so long as the otolith of the recessus utriculi remains uninjured.

The otolith of the recessus utriculi is, in the dogfish, an oval or nearly circular mass, 3 or 4 mm. in diameter, shaped like a planoconvex lens. Its convex surface rests upon the corresponding concave surface of the macula in the bottom of the recessus. I have described it as resting on the macula, but the relation of its edges to the membranous walls suggests the idea that it is in reality partially suspended. To one who is actually performing these experiments it is a remarkably striking fact that all the functions performed by the ampullæ of the vertical canals can also be performed by this one organ. In the case of the ampullæ each one has a highly specialized function,

responding to rotation in a single plane. The otolith-organ, on the contrary, responds to rotations in all planes except the horizontal.

It was natural to suppose that the pressure of the otolith is the normal stimulus for the macula. A rotation of the head would shift the weight of the otolith; change of pressure upon the macula would excite impulses in a different set of hair-cells or nerve endings, and these impulses would give rise to the compensatory movements. This idea does not differ from the original conception of Goltz of the mode of action of the ampullæ and canals, except in the unessential detail that in the one case the pressure is due to the weight of a liquid and in the other to the weight of a solid. (This is apparently the same kind of difference which exists between the otolith-containing otocyst of the crayfish and the otolithless otocyst of the crab; structures which appear to have identical functions.)

Notwithstanding the fact that we had been compelled to abandon the pressure theory of the function of the ampullæ, the pressure theory of otolith stimulation still seemed the most reasonable, until the stimulation experiments described in a preceding chapter showed that this, too, is untenable.

When we apply light pressure to one side of the otolith of the recessus we excite a reaction which is just the opposite to that which is produced by inclining the head to the same side; thus, when we press on the right side of the otolith the right eye is depressed and the left eye is elevated; but, when we turn the right side of the head downward, the right eye is elevated and the left eye is depressed. At first sight it would appear that in

the two cases the mechanical conditions are alike, that in each an increase of pressure has been applied to the right side of the macula, and that we should expect the reactions to be alike in both. That the mechanical conditions are not alike, however, will be seen from the following considerations:

The lower surface of the otolith has a curvature which is approximately spherical and the macula on which it rests forms a corresponding spherical depression. This could be represented by a convex lens, C, (Fig. 9, A.) lying in a concavity of equal curvature in the block, V. If we rotate V to the right, so as to depress its right side and elevate its left side, then C will tend, both on account of its weight and on account of its inertia, to be displaced with reference to V in the direction *lr*. The rotation will thus produce a displacement to the right, and on account of the weight of C, an increased pressure in the region *g*. If, on the other hand, we allow V to remain in the horizontal position and we press down on the left side of C in the direction of the arrow, O, (Fig. 9, B.) then C will be again displaced in the direction *lr*, but the increase of pressure will be in the region *b*. Thus pressure on the left side of the otolith causes the same displacement as rotation to the right, while it causes the opposite pressure effect on the macula. It follows that the reaction in the living animal must be caused by the displacement or the change of the tension, and not directly by the change of pressure.

It has been stated above that rotation would tend to produce a displacement of the otolith in two ways, namely, by the direct gravitational effect, or weight of the otolith, and also by its inertia. On account of the high

specific gravity of the otolith attention seems mostly to have been centred on its weight rather than on its inertia, and hence the tendency has been to lay emphasis on its fitness to be a static organ. But greater weight of course

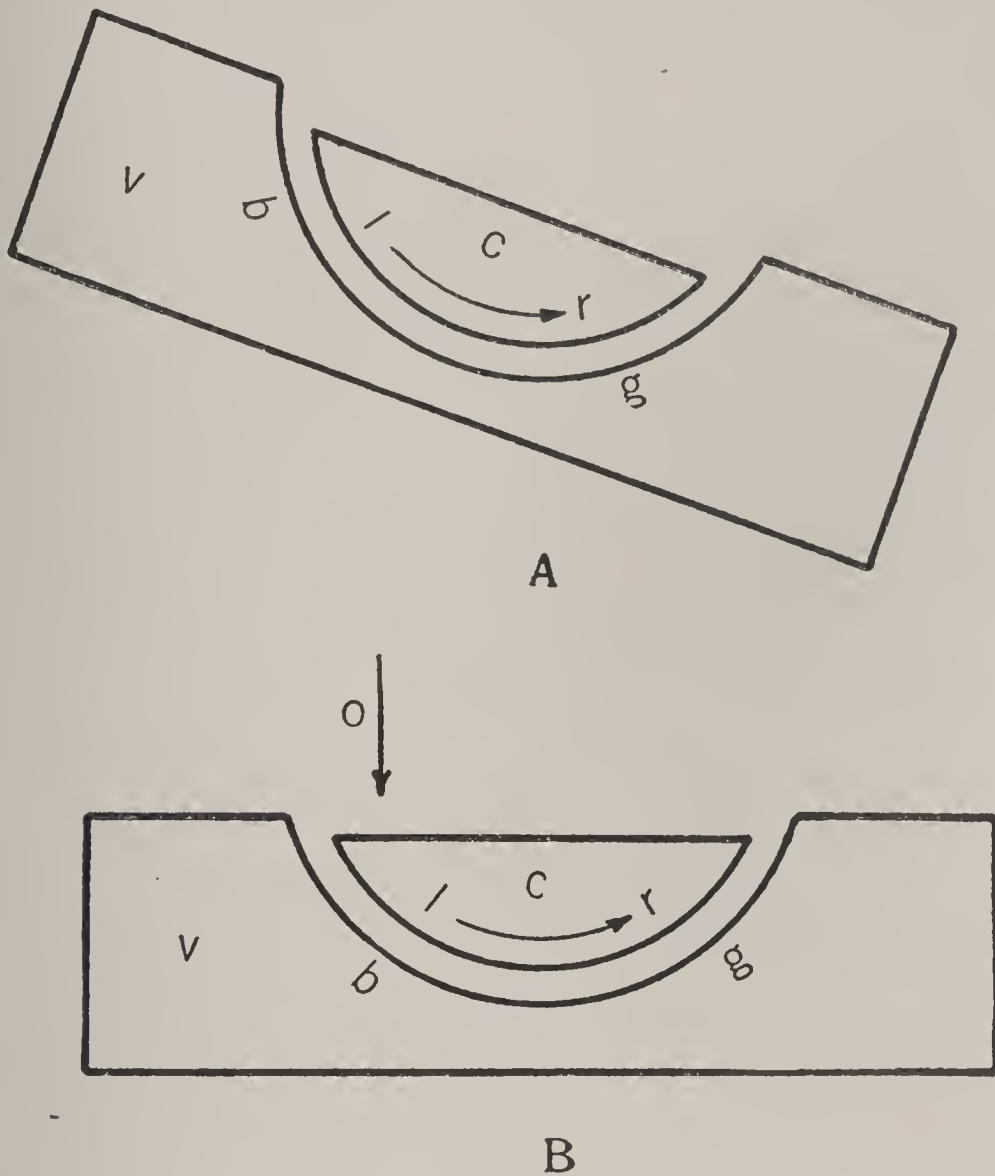


FIG. 9.

confers on it greater inertia, and for this reason, it would seem better fitted than the liquid contents of the vestibule to be a dynamic organ. So far as I have been able to observe, there is little difference between them; an animal with vertical ampullæ functional, but without otoliths, and an animal without vertical ampullæ, but with the

otolith-organ intact, react about alike to rotations around the longitudinal and transverse axes; both react in the usual fashion of a normal animal, but both react less promptly. The advantage of the greater specific gravity of the otolith seems to be just about balanced by the advantage of the larger amount of lymph in the vestibule.

A comparison of the conditions of excitation in the ampullæ and in the otolith-organ shows that both depend upon the same principle; both are affected by displacements which could produce changes of tension. It is not unreasonable to suppose that these tension changes can give rise to impulses in a manner which may be analogous to the excitation of the vagus endings in the lungs. There is nothing to prove or disprove the idea that the bending of the hair-cells is a necessary step in the process. It is hard to see just how that hypothesis could be put to the test of direct experiment. There is nothing, so far as the writer can discover, to justify the assumption of localized functional differences in the different parts of a single crista or macula; such an assumption is not needed, and should not be accepted unless supported by observed facts.

CHAPTER IX

THE MECHANISM OF THE STATIC FUNCTIONS OF THE LABYRINTH

THE facts presented in the preceding chapter show that the mechanisms of the ampullæ and of the otolith-organs act on the same general principle in the production of compensatory movements. In each case a rotational movement of the head gives rise, through inertia, to a displacement of some structure in the labyrinth, and this in turn causes a change of tension upon the nerve endings. If the rotation is stopped without a return of the body to the normal posture, the eyes and fins tend to remain in the new position at which they have arrived, and thus the compensatory movement is followed by a compensatory position. The production of the compensatory movement is the dynamic function and the maintenance of the compensatory position the static function. The experiments of the writer have shown that, in the dogfish at least, both these functions can be performed both by the ampullæ and by the otoliths. There seems to be no necessity for the terms “statolith” and “statocyst.”

It is hardly possible to conceive of the static function as anything more than a continuation of the effects produced through the activity of the dynamic function. We have seen that a displacement with its consequent change of relative tensions is the stimulus which causes the movement. If the displacement is maintained for any length

of time one may suppose that the stimulation will also be maintained. A static organ would differ from one which is only dynamic in the possession of a mechanism which would maintain the displacement that gives rise to the compensatory movement. It will be simpler to discuss this first in the case of the otolith-organ.

1. THE STATIC FUNCTION OF THE OTOLITH.

DELAGÉ⁷¹ was the first to show by actual experiment the static functions of the otoliths in invertebrates, and the proof of this was made still more complete by the remarkable experiment of Kreidl.^{127a} The otocyst of the decapod crustacean, *Palaemon* is situated in the basal joint of the small antenna and is open to the exterior. When the animal molts, the lining of the otocyst is lost and with it the otoliths, or ear sand. In these animals the ear sand consists of particles of extraneous matter, usually grains of sand, which the *Palaemon* picks up with its forceps and places in the cavity of the otocyst. Kreidl put the young crustaceans at molting time, in dishes containing magnetic sand. After particles of this material had been placed by them in the otocysts, the animals could be caused to assume forced positions by placing the magnet near them, and when the position of the magnet was changed the forced position changed accordingly.

The idea of Delage and of Kreidl was that the pressure of the otoliths upon the hair-cells acts as a constant stimulus. When the body is inclined so that the weight is shifted to a new position or acts in a new direction, the resulting pressure causes a different stimulus, affect-

ing the comparative degree of contraction of certain muscle groups; or, to state it in other words, the relative tonus of the groups of muscles concerned in maintaining the habitual posture of the animal is altered when, by a change of position of the body, the pressure of the otolith is shifted to a different set of hair-cells, and this alteration of tonus is seen in the compensatory position. In Kreidl's experiment the pressure of the magnetic particles was changed from the vertical to a direction which was the resultant of the force of gravity and the attractive force of the magnet.

The above conception needs only to be modified, on account of the results described in the preceding chapter, so as to recognize that it is not the pressure or weight which acts directly as the stimulus, but the changed relation which I have spoken of as tension; this could be a stretching or a compression of nerve endings or a bending of the hair-cells.

If this view is correct, the weight of the otolith comes into play as the means of retaining the displaced position which has been reached, and in this way the tension is maintained. When, for example, the head has been inclined to one side and held so, the tension caused by the displacement which the otolith suffers on account of its weight, acts as a stimulus, and the otolith, on account of its weight likewise, remains in the new position. It is not merely a play on words to say that the weight or pressure of the otolith is not the stimulus, but only the means to continue the displacement which is the real stimulus. This is clear if one considers the effect of pressure applied to the edge of the otolith of the recessus,

where the increase of pressure is on one side of the otolith, but the displacement is to the opposite side, and where the compensatory movement is in the direction which corresponds to the displacement and not to the increase of pressure.

2. THE STATIC FUNCTION OF THE AMPULLÆ

THE absence of otoliths in connection with the cristæ has led to the *a priori* conception of the ampullæ as only dynamic in function. The structural difference between the ampullæ and the maculæ, however, is closely paralleled by the difference between the otocysts of the crab, which possess no otoliths, and the otolith-containing otocysts of the crayfish and lobster. All of these apparently possess both dynamic and static functions. It may be, however, that the vertebrate maculæ, with their heavy otoliths, and the otolith-organs of the crayfish are more effective static organs than the vertebrate cristæ and the otocysts of the crab. No quantitative comparison of the sort, so far as I know, has ever been reported.

While an animal is undergoing rotation around a body axis there is brought about, through inertia, a displacement of the contents of the vestibule, and this displacement and the consequent change of tension acts as a stimulus. If on cessation of the movement of rotation the contents of the vestibule returned at once to their original position, the stimulus would cease and the eyes would return to the primary position. If, however, the new position of the vestibular structures continued to exist after cessation of the movement the tension differences would also continue and the resulting stimuli would give

rise to sustained forced position of the eyes; *i.e.*, to the static effect. The latter condition could exist in case the specific gravity of the utricular tissues is greater than that of the lymph. This I have found to be the case.

In most selachians the lymph of the vestibule is in free communication with the exterior sea water through the ductus endolymphaticus. It is reasonable therefore to expect that the density of the lymph would be practically equal to that of sea water. On this assumption I determined the relative weights of the membranous labyrinth and sea water by dropping small bits of utricle, ampullæ, and semicircular canals into a tall jar of sea water and saw that they all sank to the bottom. In order to be more certain, however, I succeeded in getting a sufficient amount of lymph from the ears of several fish killed at one time and dropped bits of the membranous labyrinth into it, with the result that they sank just as in sea water.

Since the membranous labyrinth and the lymph differ in specific gravity it is evident that when the membrane is displaced to a relatively lower position, its weight will have the tendency to prevent its return to the original position in the cavity as long as the new body position is retained. I believe that this difference in weight, then, is the cause of the continued forced position in the absence of the otolith.

It has been frequently stated that the stimulation of an ampulla gives rise only to a momentary movement, not to a sustained forced position, and that therefore its function can be only dynamic and not static. I have found the contrary to be very definitely true. Sustained mechanical stimulation of an ampulla, even the ampulla of a horizontal canal, causes a sustained forced position

of the two eyes; namely, a conjugate deviation to the side opposite to the stimulated ampulla. It is self-evident that in the ordinary functioning of the horizontal ampulla, when the rotation to which it responds is in a horizontal plane, no changed relation to gravity can occur and hence the reaction to rotation cannot continue after the rotation has ceased. That the horizontal ampulla reacts to its normal stimulus by a response then is due only to its space relations, and not to a different kind of physiological function. Of course my experiments have demonstrated the ability of the other ampullæ to produce sustained static effects.

CHAPTER X

THE TONUS EFFECTS OF THE CRISTÆ AND OF THE MACULÆ

As THE result of numerous investigations on the physiology of the labyrinth, Ewald arrived at his celebrated tonus theory. He laid emphasis upon the discrimination of two parts, the auditory labyrinth and the tonus labyrinth, with distinct and very different functions. By many beautiful experiments he established, beyond question, the fact of an influence of the labyrinth upon the tonus of the many body muscles. His theoretical deductions were less happy. He assumed the presence of continuous ciliary activity on the part of the hair-cells and this ciliary movement was in some way associated with muscle tonus. His attention was almost wholly centred on the canals and ampullæ; the otoliths were dismissed with some *a priori* considerations.

The equilibrium reactions were subordinate to the tonus effects. The ciliary activity of the hair-cells was augmented by an increased flow of endolymph in one direction with a consequent increase of their tonic influence and hence a contraction of certain muscle groups, while an opposite flow of the current caused a checking of the movement of the hair-cells and an inhibition of tonus. We do not yet know what tonus really is nor how it is excited through the labyrinth. It is better to be content with the facts than to assume an unnecessary hypothesis.

Ewald's original conception of the tonus labyrinth applied only to the canals and ampullæ. Later his pupil,

Ach,¹ spoke also of an otolith tonus, but for its existence he gave no clear evidence. Through a series of painstaking investigations carried on for more than a decade, Magnus and de Kleijn have drawn attention to a most instructive array of details concerning the tonus of the various muscle groups and the dependence of their tonus on various factors, chief among which is the influence of the labyrinth. They have shown, for example, that in the rabbit, when the disturbing and inhibitory effects of the cerebral hemispheres are excluded, definite tonus changes of the muscles of the neck, trunk, limbs and eyes take place with each change of position of the body. These tonus changes can be excited through different stimuli which normally coöperate and reënforce each other. Thus when the rabbit is placed upon its side, the labyrinth gives rise to excitations which cause an unsymmetrical distribution of tonus in the neck muscles so that the head is brought into a position of symmetry with reference to the lines of gravitational force. The altered position of the head is now asymmetrical with reference to the trunk; and the changed pressures and tensions in the joints or muscles of the neck act reflexly to bring about tonus changes in the muscles of the trunk and of the limbs in such a way as to raise the body into the normal posture. In addition to these sources of afferent impulses contact stimuli arising from the side on which the body lies, tend also to cause the lifting of the head and, indirectly, the raising of the body into a position of symmetry.

De Kleijn and Magnus have, on the basis of their observations, drawn a sharp distinction between reflexes which they consider to be excited by movement and those

which are excited by position. This is essentially the old distinction of dynamic and static reactions. These authors have assumed that the dynamic reactions, excited by angular accelerations, have their origin in the cristæ of the canals, and that the posture reflexes, on the other hand, depend upon the state of excitation of the maculæ. According to this conception the tonus effects, assigned by Ewald to the ampullæ, are chiefly dependent on the maculæ with their otoliths.

I have pointed out in a preceding chapter that the excitation which brings about a posture reflex must be dynamic as well as static; the muscles must cause a movement in order that there shall be a new position to sustain, and hence the difference between dynamic and static is only a difference of the presence or absence of a mechanism for the continuance of the excitation and so of the state of muscular tonus. If this conception is correct we should expect to find that both cristæ and maculæ are capable of maintaining tonus. In case there is a real physiological difference in the kind of excitation aroused in the cristæ and in the maculæ, then, according to the conception of the latter as to the source of posture reflexes, we should expect to find tonus effects only from the maculæ. The certainty with which either ampullæ or otoliths can be removed in the dogfish makes this animal especially useful for the investigation of the question.

When one labyrinth of the dogfish is completely destroyed, a difference of tonus on the two sides of the body is evidenced by the unsymmetrical position of the body, eyes and fins. Loeb¹⁴³ saw that when the otoliths were removed from one ear, the position resembles that of an animal with the eighth nerve cut. Lee¹³⁷ stated that

when the ampullar branches of the eighth nerve were sectioned on one side, an unsymmetrical position resulted; the body was inclined to the operated side, the eye on the operated side was depressed, and the eye on the other side elevated. He also saw in animals in which he had washed out the otoliths from one ear a similar asymmetrical position. If we may judge from these observations, tonus effects which are not merely momentary but sustained, can originate in both the cristæ and the maculæ. I have investigated this matter, using the more exact extirpation methods described in chapters VI and VII.

(1) When all three ampullæ are removed from the right ear of a dogfish, the asymmetrical positions of body, eyes, and fins are very similar to those assumed when the whole labyrinth has been destroyed; namely, the body is inclined to the right, the right eye is depressed and the left elevated, the dorsal fins are turned to the left, and the paired fins on the right are elevated while those on the left are depressed. In this condition, the animal's activities seem little affected; it goes deeper or to the surface, turns to the right or to the left like a normal specimen, although the asymmetry is permanent. If now we remove the three ampullæ from the left ear, the asymmetry disappears, and the condition is established which we have previously described. The animal maintains its equilibrium, rights itself when turned over in the water, and shows normal, but somewhat weakened compensatory movements to rotations in all planes except the horizontal. These reactions show that the otolith-organs were not injured by the operation.

So long as the ampullæ were present in one ear and missing from the other, the asymmetrical placings of the eyes and fins gave evidence of a continuous tonic influence from the ampullæ of the sound ear.

(2) All the ampullæ were removed from both ears of the dogfish and after making sure that no asymmetrical injury had been done to the labyrinths, as shown by the normal posture of the animal, the otoliths were removed from the right ear. The animal continued to maintain fairly well its equilibrium in water, righted itself when turned over, and showed hardly any noticeable asymmetry of position. This makes it probable, in fact almost certain, that the asymmetry seen by previous observers on washing out the otoliths from one ear was, in reality, due to the incidental injury to or destruction of the connections of the ampullæ with the vestibular structures, and was due mainly or wholly to a lack of balance of ampullar, not of otolith, tonus effects.

(3) We remove the ampullæ from the right ear and observe the degree of asymmetry which follows the operation; if we now complete the destruction of the right labyrinth by washing out the otoliths, the asymmetry is not noticeably, or but very slightly, increased. Unfortunately, no reliable method of determining quantitatively the degree of asymmetry could be hit upon.

(4) When the otoliths are removed from one ear with a minimum of injury to other structures the results are as described in 2, above. An asymmetrical position rarely occurs; but when it does it is probably in a specimen whose utriculus and sacculus have been injured in the operation.

A comparison of the four classes of experiments just described makes it evident that the ampullæ are the seat of continuous tonic influences. When the ampullæ of one ear are lacking, a tonus difference appears on both sides of the body. It would be incorrect to assume, as has been done by many writers, that the cristæ of each labyrinth have a predominating influence on one side of the body. As we have pointed out with reference to one-sided destruction of the whole labyrinth, the asymmetry is due to an influence on muscles on both sides of the body in such a way that the tonus of muscles of one side is decreased while that of the antagonists of the corresponding muscles on the other side of the body is also decreased. When, for example, the ampullæ are removed from the right ear, the muscles which lower the right pectoral fin and the muscles which raise the left pectoral act more weakly than normal with the result that the fin on the right side is elevated and its fellow on the left is depressed.

The question of the tonic effect of the otoliths is not so easy. At first sight it might seem that the almost complete absence of asymmetry after destruction of the otoliths in one ear shows a lack of tonic influence of the macula. It must be remembered, however, that displacements of the otolith of the one ear can cause compensatory movements in both directions; and that these movements, in the rays, and apparently also in the dogfish, are brought about alike by displacement of the otolith in either the right or the left ear. From this it would appear that symmetrical tonus effects may be produced by the macula of the one ear. In this case an asymmetrical operation would not give rise to differences of tonus in

the homologous muscle groups on the two sides of the body, and hence we could not by this method arrive at conclusions of otolith tonus in general.

The above described experiments then give us positive evidence of the tonic influence of the ampullæ but are not capable of solving the problem of otolith tonus. De Kleijn and Magnus¹²¹ have attempted to find the solution in an interesting manner. As a basis for their work a careful determination was made by de Burlet and Koster⁵⁴ of the form and orientation of the otoliths of the ear of the rabbit. From the data thus obtained a model was constructed which could be used to show the position of each otolith and macula, or otolith membrane, for every position of the head. Assuming that the labyrinth posture reflexes originated in the maculæ, they studied the tonus of various muscle groups for the different positions of the head and sought to correlate these with the orientation of the otoliths in each position. The following will serve as an illustration of the method:

In a decerebrated rabbit the extensor muscles of the limbs are in an especial state of tonus, decerebrate rigidity. This tonus depends upon, or is strongly influenced by, the labyrinth. It is found by rotating the body around the transverse axis that there is one and only one position of the animal at which the tonus of the limbs is maximal, namely, when the animal is in the position back downward with the line of the mouth-opening horizontal or elevated not more than 45 degrees. There is also another position in which the tonus is at a minimum, and this always differs from that of maximum tonus by 180 degrees. Comparing these positions with the planes of the different otoliths no definite relations are found for

those of the sacculus. The otoliths of the utriculi, on the other hand, lie nearly in one plane, and are so situated that when the extensor tonus is at its minimum the otoliths are horizontal and resting upon the maculæ, when the tonus is at its maximum the otoliths are horizontal but hanging from the maculæ. Assuming that the tonus changes are actually excited from the maculæ, de Kleijn and Magnus conclude that it is not the pressure of the otolith which acts as the stimulus, but on the contrary the pull or tension which it exerts. This conclusion, reached by an indirect method, is in close accord with what has been proved by the writer through direct experiment upon the labyrinths of fishes.

Applying a similar method of analysis through the study of maximal and minimal tonus for various muscle groups, eyes, limbs, neck, trunk, etc., these authors have assigned specific tonus functions to the otolith of the utriculus, to the larger portion of the saccular otolith, and to a smaller, angular portion of the same otolith, lying in a different plane. For all the positions of all the otoliths the conclusion was reached that the maximal excitation occurs when the *macula is horizontal and the otolith hangs below it*.

When we compare the conclusions arrived at by de Kleijn and Magnus on the functions of the different otoliths with the results obtained by the writer, a marked contrast appears in the rôle of the otoliths of sacculus and utriculus in the rabbit and in the fish; for in the fish all the position reflexes can be obtained from the otolith of the utriculus alone. The same may be true in the rabbit since the method of study through maximal and minimal tonus depends upon *a priori* considerations, and

a priori reasoning has led to a multitude of misconceptions before in the study of labyrinth function. De Kleijn and Magnus have wisely remarked that their conclusions can be applied at present only to the rabbit. The relations in other mammals remain to be worked out; while in animals with three otoliths in each ear, the individual functions must be different. We may agree with the last statement, only we should say "may be," not "must be" different.

CHAPTER XI

NYSTAGMUS

SOME confusion exists in the use of terms descriptive of nystagmus. In nystagmus excited through the ear it is usually easy to determine that one phase of the oscillation is identical with the compensatory motion which would result from the stimulation of the labyrinth. The other phase consists of a quick return to or toward the primary position. The former of these was called by Ewald the reaction phase and the latter the nystagmus phase. The compensatory phase is generally slower than the return, and for this reason the two movements are often spoken of as the slow component and the quick component respectively. Following Ewald's use of the expression "nystagmus-phase," it is common for writers to speak of the direction of the return movement as the direction of the nystagmus; thus, when a man is turned to the right in a revolving chair his eyes, during the rotation, make slow movements to the left and quick returns to the right; such a nystagmus is commonly, but not uniformly, described as nystagmus to the right. The writer has no desire to urge the use of a different terminology, but believes that in this chapter confusion will be avoided by referring to the two constituent phases as the *compensatory* and the *return* movements or phases.

Since the direction of a compensatory movement depends upon the plane of rotation which calls it forth, the nystagmic movements must also depend upon the plane of

the rotation, and hence may be horizontal, vertical, or rotary, or a resultant of any two of these. We must also distinguish between the nystagmus which occurs during a rotation and the after effect, the after-nystagmus, which occurs on cessation of the rotation.

When a dogfish is rotated very slowly in the horizontal plane, a typical nystagmus may be seen; the eyes for a moment make the characteristic compensatory movement in the direction contrary to the rotation and then suddenly come back toward the primary position. If the rotation is made more rapid, only the compensatory movement occurs, the return movements do not appear. The same phenomena may also be seen in the pigeon and other animals, only the rotation has to be more rapid in order to cause the omission of the return movement. From this it would appear that the two phases are not only physically opposite but mutually inhibitory. When the labyrinthine excitation is sufficiently powerful it overcomes the inhibitory effect of the impulse for the return movement and *vice versa*.

The nystagmus of the eyes and the nystagmus of the head excited by rotation must be considered together. Fundamentally the two present the same phenomena. When we rotate a pigeon or a rabbit on the turntable, a marked compensatory position of the head, or a head-nystagmus, occurs. If the head is forcibly retained in the median position so that its movement is prevented, the eye-nystagmus becomes more rapid and intense. Bartels²⁴ found that this is also true of very young infants.

The compensatory phase is very evidently the kind of reaction which is excited through the labyrinth. The origin of the return movement is not so clear. It has

been supposed to be of cerebral origin but for reasons which are not very convincing. In a certain depth of narcosis the return movements are abolished while the compensatory phase continues to be exhibited. The same phenomenon is also seen in sleeping infants and in infants prematurely born. None of this, however, is proof. We do not know with precision the gradation of the effects of narcotics on the cerebral cortex, basal ganglia, brain stem and other parts of the nervous system; nor do we know any better the actual level of the brain which forms the line of physical demarcation between consciousness and unconsciousness; but we do know that sleep does not depend upon the cerebral hemispheres. On the other hand, Ewald⁷⁵ had found that in the pigeon the nystagmus is not affected by the loss of the cerebral hemispheres, and Bauer and Leidler²⁸ and Magnus¹⁵⁶ found the same to be true in the mammal. It is, therefore, incorrect to speak of the return movement as a cortical reflex.

Since the time of Flourens, who called attention to the general resemblance of the symptoms which follow injuries to the cerebellum and to the labyrinth, it has been rather common to assume that the effects of the labyrinth are produced through the cerebellum. This view has been expressed in one form or another by Bechterew,³¹ Luciani,^{147a} Bárány,¹⁸ and many others. This has been shown very definitely to be erroneous. Lange¹³⁵ found that, in pigeons, the head nystagmus occurs in a perfectly characteristic way after destruction of the cerebellum. Moreover, the effects of labyrinth destruction and of cerebellar injuries have only a superficial resemblance; they differ in very essential details. Beyer and Lewand-

owsky³⁶ found that, in mammals, after extirpation of the cerebellum, the destruction of one labyrinth still produced the typical asymmetrical disturbances. Labyrinth effects were neither produced nor prevented by loss of the cerebellum, nor did destruction of the labyrinths prevent the typical results of subsequent cerebellar injuries. Finally de Kleijn and Magnus¹¹⁷ have shown that the labyrinthine reflexes, including the nystagmus produced by rotation, occur normally in the absence of the cerebellum.

In both the compensatory and the return phase the eye muscles conform to the principle of reciprocal innervation. While, for example, the rectus externus is actively contracting, the rectus internus is not just passively stretched, but it undergoes a relaxation which is as definite a physiological process as the contraction. This is well shown in the experiments of Bartels²⁵ on the eye muscles of the rabbit. He arranged a small kymograph on the turntable so as to secure a graphic record both of the rotation-nystagmus and of the after-nystagmus. The rectus externus and the rectus internus were dissected loose from their attachments to the eyeball and were connected by means of threads to two light levers. In this way the state of contraction or relaxation of each muscle was recorded independently of the other; the contraction of the one could not passively stretch the other.

The curves obtained by Bartels show that during the compensatory phase the one muscle makes a relatively slow contraction while its antagonist relaxes at a corresponding rate. When the contractions of the rectus

internus and externus of the left eye were recorded during rotation to the right, the externus slowly contracted and the internus relaxed during the compensatory phase. This was followed by the return movement which consisted of a quick contraction of the internus and a correspondingly quick relaxation of the externus. When the rotation was stopped the after-nystagmus showed, as might be expected, exactly the reverse relations. Bartel's curves show that contraction of a muscle and relaxation of its antagonist keep pace very closely; a slow contraction of the one is accompanied by a slow relaxation of the other, while a quick contraction is accompanied by a quick relaxation.

We have seen that changes of tension or pressure on the nerve endings in the muscles or joints of the neck can excite movements of the eyes. This may give a hint as to the nature of the origin of the return movement. We cannot, however, ascribe the return movement to the direct effect of the stimulus in the neck; for the neck itself can give rise to an eye-nystagmus which like the nystagmus of labyrinthine origin is made up of a compensatory and a return phase and we have still to find the seat of the excitation for the return phase of this. It is not impossible that the excitations for the return phases in both are to be found in the muscles and tendons concerned in the movement. When we bend the head of a rabbit to the left the eyes make compensatory movements to the right. If the head is held in the forced position the eyes retain a compensatory position, although the amount of deviation is less than the extremes attained

during the bending of the neck. Ewald⁷⁵ described a similar phenomenon in the dog but with this striking difference, that the compensatory position of the eyes continues so long as the dog makes the effort to return the head to the line of the body. As soon as he gives up the effort the eyes come back to the primary position. One can feel with the fingers the moment of the relaxation and see that it coincides with the change in the position of the eyes. These facts seem to indicate that the stimuli are peripheral and arise from tension in the muscles and tendons rather than from pressure in the joints.

Bartels²⁵ is inclined to find the stimulus for the return movement of the eye-nystagmus in the eye muscles themselves. Section of the branches of the trigeminal nerve through which afferent impulses from the orbit and bulb could come does not interfere with the course of the nystagmus. The nerves which supply the muscles of the eyeball have been supposed to be purely motor; but Tozer and Sherrington²³² found that these nerves carry sensory fibres also to the eye muscles. Bartels believes that through these fibres pass the impulses which produce the return movement.

There remains another possibility as to the origin of the return movement. Some portion of the central nervous system may be capable of exerting a tonic influence the effect of which is to tend to keep the eyes in the primary position and to bring them back to this position when, through any stimulus, they are moved away from it. De Kleijn¹¹³ has presented the following evidence in support of this view. The rectus externus muscle of the left

eye of a rabbit was detached from the eyeball and connected with a lever so that a graphic record could be obtained. The cerebral hemispheres of the animal were removed and the brain stem cut through just in front of the anterior corpora quadrigemina. The third and fourth cranial nerves of both sides and the sixth nerve of the right side were then sectioned. The application of caloric stimulation to the ear still caused the characteristic contractions of the rectus muscle, including the quick contractions which normally cause the return movement. The conditions of the experiment still left one pathway for the coming in of peripheral impulses; the sixth nerve of the left side which, of course, had to be spared to conduct the motor impulses. De Kleijn sought to put the efferent fibres of this out of action by the injection of a one per cent. solution of novocain, which ordinarily paralyzes the sensory nerves at a time while the motor nerves are still functional. In this experiment, however, the two sets of impulses, compensatory and the return, disappeared at the same time. This result is indeed very suggestive, but it does not appear to the writer to furnish positive proof of the central origin of both sets of impulses.

Though we may assume that movements of rotation are the physiological stimuli for the labyrinth, other stimuli also can act upon it. Thus when a current of water some degrees warmer or colder than body temperature is caused to flow into and out of the external ear, so that the temperature of the tympanic region is made to be different from that of the neighboring parts, the so-called caloric reaction is produced; a conjugate deviation of the eyes or a nystagmus occurs, the direction of which de-

depends upon the temperature of the water. When water is used which is warmer than the body, the compensatory phase is in the direction away from the stimulated side; when the water is colder than the body, the compensatory phase is toward the stimulated side.

An attempt has been made to account for the caloric nystagmus on the basis of the tonic influences of the labyrinth, and the effects of heat and cold on the excitability of the sensory elements. If the sensitivity, and the tonic activity, of the labyrinth is increased by a rise of temperature, then the douching of the right ear with water should cause the influence of the right ear to exceed that of the left and produce a conjugate deviation of the eyes to the left; douching the right ear with cold water should reduce the sensitivity of the right ear below that of the left with the result that the effect of the left labyrinth would predominate and a deviation to the right would occur. It only needs that the reflex apparatus which causes the return movement be active in order that a nystagmus should occur in accordance with the observed facts.

The above explanation without further modification fails, however, to account for another very striking part of the phenomenon, namely, that while the caloric nystagmus is in progress a change in the position of the head causes a change in the direction of the nystagmus. Thus when the head of the human subject is tilted backward 60 degrees, bringing the horizontal canals into an approximately vertical plane, syringing the right ear with cold water causes a nystagmus in the plane of those canals, with the compensatory phase to the right. If now the head is inclined forward 120 degrees, the horizontal

canals are again in a vertical plane, but the compensatory stroke of the nystagmus is to the left. Bárány¹⁵ and Brünings⁵² have attempted to account for the phenomena of caloric stimulation on the assumption that the application of heat and cold produces a change of density in the

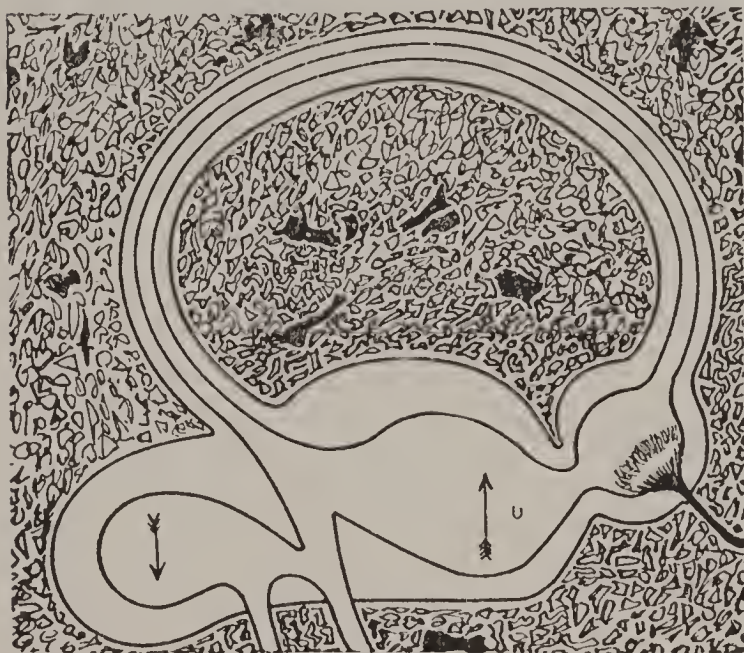


FIG. 10.—Diagram to illustrate the principle of caloric stimulation.

outer portions of the semicircular canals, and that this change of density causes, through the action of gravitation, currents in the canals which stimulate by deflection of the hair-cells. The change in the position of the head changes the direction of the current and hence the nature of the stimulus.

Maier and Lion¹⁶⁵ have shown that in a glass model of the size of the human canals, a perceptible and long lasting current can be produced by temperature differences comparable to those used in douching the ear, and they believe that by this they have proved that similar currents are the cause of the caloric stimulation. We have seen, however, that the normal excitation of the ampulla can occur when no current is possible in the canal. Moreover, a difference in temperature sufficient to cause a current in a canal must produce still greater disturbance of equilibrium in the larger mass of liquid in the vestibule with consequent tension effects upon the membrane labyrinth. The liquid in the vestibule is not wholly free, but

is partly enclosed in the utriculus and sacculus in such a way that the heavier or lighter fluid must be held in one portion of the vestibule and by the difference of weight exert tension on the membranes. In this way a mechanical stimulus takes place exactly comparable to that which,

as we have previously seen, is produced by rotation. By referring to Fig. 10, it can be seen that the application of heat to the parts represented by the right hand side of the figure would cause a decrease in density of the liquid in region *U* and this would give rise to changes in tension acting in the directions indicated by the arrows.

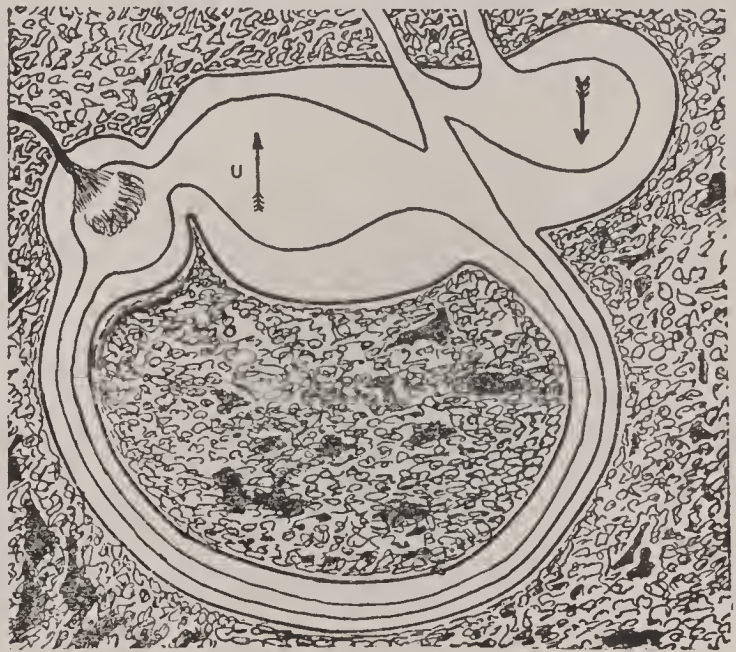


FIG. 11.—Diagram to explain effect of change of position on the head on the result of caloric stimulation.

If cold instead of warmth were applied, the density would be increased in region *U* and the tension effects would be the reverse.

Changing the position of the head must also change the direction of the pressure due to differences of density of the liquid in the vestibule. If, for example, the right hand side of the structures has been warmed, and the density and tension changes indicated in Fig. 10 have been produced, changing the position by 180 degrees (Fig. 11) must, through the influence of gravity, exactly reverse the relative tensions, with a consequent change in the application of the mechanical stimuli and in the nature of the resulting nystagmus.

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* With the exception of certain papers containing the fundamental observations, this list includes only literature which has appeared since Ewald's monograph. Articles based wholly on clinical or psychological data have mostly been omitted.

A complete bibliography of the labyrinth has been compiled by Dr. C. R. Griffith; it is hoped that this will soon be made available through its publication.

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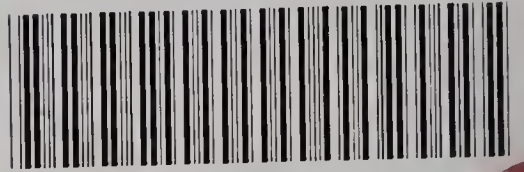


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